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AJO PEAK TO TINAJAS ALTAS: A FLORA IN SOUTHWESTERN ARIZONA. PART 7. EUDICOTS: CACTACEAE – CACTUS FAMILY

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ABSTRACT

A floristic account is provided for the cactus family as part of the vascular plant flora of the contiguous protected areas of Organ Pipe Cactus National Monument, Cabeza Prieta National Wildlife Refuge, and the Tinajas Altas Region in the heart of the Sonoran Desert in southwestern Arizona. The modern native cactus flora includes 35 taxa in 12 genera, plus 2 non-native prickly-pears that are not established in the flora area. The overall cactus flora including fossils and non-natives totals 39 taxa in 13 genera: at least 17 taxa are represented by fossils recovered from packrat middens, two of which are no longer present in the flora area. This account includes selected synonyms, English, Spanish, and O'odham common names in when available, identification keys, brief descriptions, images, local and general distributional, natural history, and ethnobotanical information. This flora is specimen-based with selected specimens cited. A new combination is proposed: **Echinocereus coccineus** Engelmann subsp. **santaritensis** (W. Blum & Rutow) M.A. Baker. *Echinomastus erectocentrus* var. *acunensis* is treated as synonym of *Sclerocactus johnsonii*. Club chollas in the flora area previously called *Grusonia kunzei* and *G. parishii* are correctly shown to be *G. wrightiana* and *G. kunzei*, respectively. Cactus diversity in the flora area generally decreases from regions of higher and more predictable rainfall (east side of the flora area) to lower and less predictable rainfall (west side of the flora area). Sixteen taxa generally do not range westward from the flora area and five do not range eastward. *Cylindropuntia*, with 12 present-day taxa, is the most diverse cactus genus in the flora area as well as the Sonoran Desert. Also included is a discussion of convergent evolution of water-conserving adaptations in *Peniocereus striatus* and an African *Euphorbia*. This is the seventh contribution for this flora series published in Phytoneuron and available on the website of the University of Arizona Herbarium.

CACTACEAE – Cactus Family

Cacti, especially organ pipe (*Stenocereus thurberi*), inspired the formation of the Organ Pipe Cactus National Monument. Some cactus species in the present–day flora are defining aspects of the landscape while others can only be seen if you diligently search for them. These cacti have provided people with significant food and beverages, the saguaro and organ pipe fruits being especially delicious and sought after. The local cacti also have been used for house construction, medicine, and for other practical as well as religious or ritual purposes (e.g., Castetter & Bell 1937; Felger 2007). The yellow-spine prickly-pear, *Opuntia engelmannii* var. *flavispina*, occurs at former village and farming sites and may represent introductions and/or selections by Native Americans.

Cactaceae is fourth largest family in the flora area (Felger et al. 2013a & b). The local cactus diversity includes 12 genera and 39 total taxa with 31 native modern species plus 1 hybrid and several varieties (Table 1). At least 18 taxa are represented by fossils recovered from packrat middens. *Coryphantha vivipara* and *Cylindropuntia multigeniculata*, collected by Ice Age packrats in Organ Pipe mountains, are not known from the flora area earlier than 9600 years ago. *Cylindropuntia*, with 12 present-day taxa, is the most diverse cactus genus in the flora area as well as the Sonoran Desert. Organ Pipe has 32 modern, present–day native cactus taxa, Cabeza Prieta has 25 taxa, and 14 occur in the Tinajas Altas region. Two prickly-pears, *Opuntia engelmannii* var. *linguiformis*, which is scarce, and *O. santarita*, which was cultivated, are the only non-native cactus reported in the flora and are not established or reproducing.

Within the study area, the diversity of cactus taxa decreases as aridity increases from east to west. Sixteen taxa do not range westward from the flora area and five do not range eastward (Table 1). For example, the red–flowered mountain hedgehog cactus (*Echinocereus coccineus* subsp. *santaritensis*), typically found in the high mountains of southeastern Arizona, occurs in the flora area only at elevations over 1000 meters in the Ajo Mountains of Organ Pipe, and does not range farther westward. In contrast, the many-headed barrel cactus (*Echinocactus polycephalus*) and beavertail cactus (*Opuntia basilaris* var. *basilaris*) do not range farther eastward in flora area than the hyperarid western part of the region.

Peniocereus striatus and *Lophocereus schottii* are at their northern geographic limits along the southern margin of the flora area and the nearby Tohono O'odham lands—their northern limits due to severity of winter freezing (see Felger et al. 2013a). Five cacti are scarce and/or of limited distribution in the flora area and therefore of local conservation concern: *Lophocereus schottii, Mammillaria thornberi, Opuntia engelmannii* var. *flavispina*, *Peniocereus striatus*, and *Sclerocactus johnsonii.* Severe drought, probably correlated with climate change, has impacted a number of local cactus populations, especially *Cylindropuntia leptocaulis*, *C. ramosissima*, *Mammillaria* spp., and *Sclerocactus johnsonii.*

The 37 present-day cacti in the flora area (Figure 1) represent 22% of the total Sonoran Desert cactus flora, which includes about 180 taxa (approximately 128 species plus 27 subspecies and varieties, and 30 hybrids) in 21 genera (Felger et al., unpublished manuscript). Wiggins (1964), in his flora of the Sonoran Desert, included 160 taxa of cactus, of which about 15 percent were infraspecific taxa. The geographic extent used by Wiggins, based loosely on Shreve's (1951) defining map, was considerably broader than newer concepts of the Sonoran Desert (e.g., Felger et al. 2001; Turner & Brown 1982). Furthermore, Wiggins included a number of cactus taxa clearly not even within the boundaries of Shreve's concept of this desert. The cactus family includes about 1800 species in 125 genera, native to the New World with a single exception (Anderson 2001).

Theft of cactus from the flora area is known to occur but the impact on local populations has not been quantified. Poaching is probably greatest along the U.S./Mexico border near Sonoyta and less common along the more remote public road systems. Some poaching undoubtedly occurs for commercial gain, but some plants are taken for personal collections or medicinal use. Although no formal records of poaching exist, a few instances are remembered. In 2002 a hole and a crumbled cigarette pack were all that remained of a tagged and geo-referenced night-blooming cereus (*Peniocereus greggii*) plant that was part of a monitoring study at Organ Pipe (S. Rutman, pers. observation). In another instance in the early 2000s, a National Parks ranger encountered a man dragging the bottom end of a chain-fruit cholla (*Cylindropuntia fulgida* var. *fulgida*) from Organ Pipe into Mexico, to use as a treatment for a stomach ailment. When asked why he couldn't get the plant in Mexico, the man replied, "Because there are no more left over there." At Bates Well in 2010, two smugglers with an unknown motive were discovered carrying a barrel cactus (*Ferocactus*) pierced by a long iron rod.

Table 1. Local distributions of cactus taxa for the flora in southwestern Arizona. † = modern taxon also represented by a fossil specimen. †† = fossil taxon not found in the modern flora area. ** = non-native and not established (not reproducing) in the flora area. OP = Organ Pipe Cactus National Monument, CP = Cabeza Prieta National Wildlife Refuge, TA = Tinajas Altas Region. Geographic limits: W = taxa generally not ranging westward from the flora area, and E = taxa generally not ranging eastward from the flora area.

Taxon	Region			Geographic limit	
	Organ Pipe	Cabeza Prieta	Tinajas Altas	W	E
†Carnegiea gigantea	OP	CP	TA		
††Coryphantha vivipara	OP				
Cylindropuntia acanthocarpa var. coloradensis	OP	CP	TA		
Cylindropuntia acanthocarpa var. major	OP				
(†Cylindropuntia acanthocarpa)	(OP)		(TA)		
Cylindropuntia acanthocarpa × C. spinosior	OP				
Cylindropuntia arbuscula	OP	CP		W	
†Cylindropuntia bigelovii	OP	CP	TA		
Cylindropuntia echinocarpa		CP	TA		E
Cylindropuntia fulgida var. fulgida	OP	CP		W	
Cylindropuntia fulgida var. mamillata	OP			W	
(†Cylindropuntia cf. fulgida)	(OP)				
†Cylindropuntia leptocaulis	OP	CP			
††Cylindropuntia multigeniculata	OP				
†Cylindropuntia ramosissima	OP	CP	TA		E
Cylindropuntia spinosior	OP	CP		W	
Cylindropuntia versicolor	OP			W	
†Echinocactus polycephalus		CP	TA		E
Echinocereus coccineus ssp. santaritensis	OP			W	
Echinocereus engelmannii ssp. engelmannii	OP	CP	TA		
Echinocereus nicholii	OP	CP		W	
(†Echinocereus sp./spp.)	(OP)		(TA)		
†Ferocactus cylindraceus	OP	CP	TA		
†Ferocactus emoryi	OP	CP		W	

†Ferocactus wislizeni	OP	CP	TA	W	
Grusonia kunzei	OP			W	E
Grusonia wrightiana	OP	CP	TA		
Lophocereus schottii var. schottii	OP	CP		W	
†Mammillaria grahamii	OP	CP	TA		
Mammillaria tetrancistra	OP	CP	TA		
Mammillaria thornberi	OP			W	
(†Mammillaria sp.)			(TA)		
†Opuntia basilaris var. basilaris		CP	TA		E
†Opuntia chlorotica	OP	CP	(†TA)		
Opuntia engelmannii var. engelmannii	OP	CP			
Opuntia engelmannii var. flavispina	OP	CP		W	
**Opuntia engelmannii var. linguiformis	OP				
(†Opuntia engelmannii &/or O. phaeacantha)	(OP)				
Opuntia phaeacantha	OP				
**Opuntia santa-rita	OP				
Peniocereus greggii var. transmontanus	OP	CP	TA	W	
Peniocereus striatus	OP			W	
Sclerocactus johnsonii	OP				
†Stenocereus thurberi	OP	CP		W	
Total taxa: 39	36	25	14	16	5
	Organ Pipe	Cabeza Prieta	Tinajas Altas	West limit	East limit

The first article in this series includes maps and brief descriptions of the physical, biological, ecological, floristic, and deep history of the flora area including references for the fossil record from packrat middens, as well as impacts due to USA–Mexico border issues (Felger et al. 2013a). In the following species accounts, the accepted scientific names are in bold and selected synonyms are italicized within brackets [--]. Common names, when known or worthwhile, are in English, Spanish, and the Hia C-ed O'odham dialect, respectively (see Felger et al. 1992 and 2007 for usage of Hia C-ed O'odham plant names). Spanish-language names are italicized. All specimens cited are at the University of Arizona Herbarium (ARIZ) unless otherwise indicated by the abbreviations for herbaria at Cabeza Prieta National Wildlife Refuge (CAB), Organ Pipe Cactus National Monument (ORPI), and the standardized abbreviations for herbaria (Index Herbariorum, Thiers 2013). Publication information is provided for taxa (accepted names and synonyms) based on type specimens from the flora area or in cases where such information augments our taxonomic decisions. We often refer to Organ Pipe Cactus National Monument as "Organ Pipe," Cabeza Prieta National Wildlife Refuge as "Cabeza Prieta," and the Tinajas Altas Region as "Tinajas Altas." We include only selected natural history and ecological information and references—the literature is far too vast to provide a comprehensive coverage; Drezner and Lazarus (2007) give an excellent overview and interpretation of much of the relevant literature.

We have seen specimens or images of all specimens cited. When no collection number is provided, the specimen is identified by the date of collection. Generally only the first collector's name is given. The two non-native cacti in the flora area are not established as reproducing populations, and are marked with two asterisks (**). Fossil specimens are indicated with a dagger

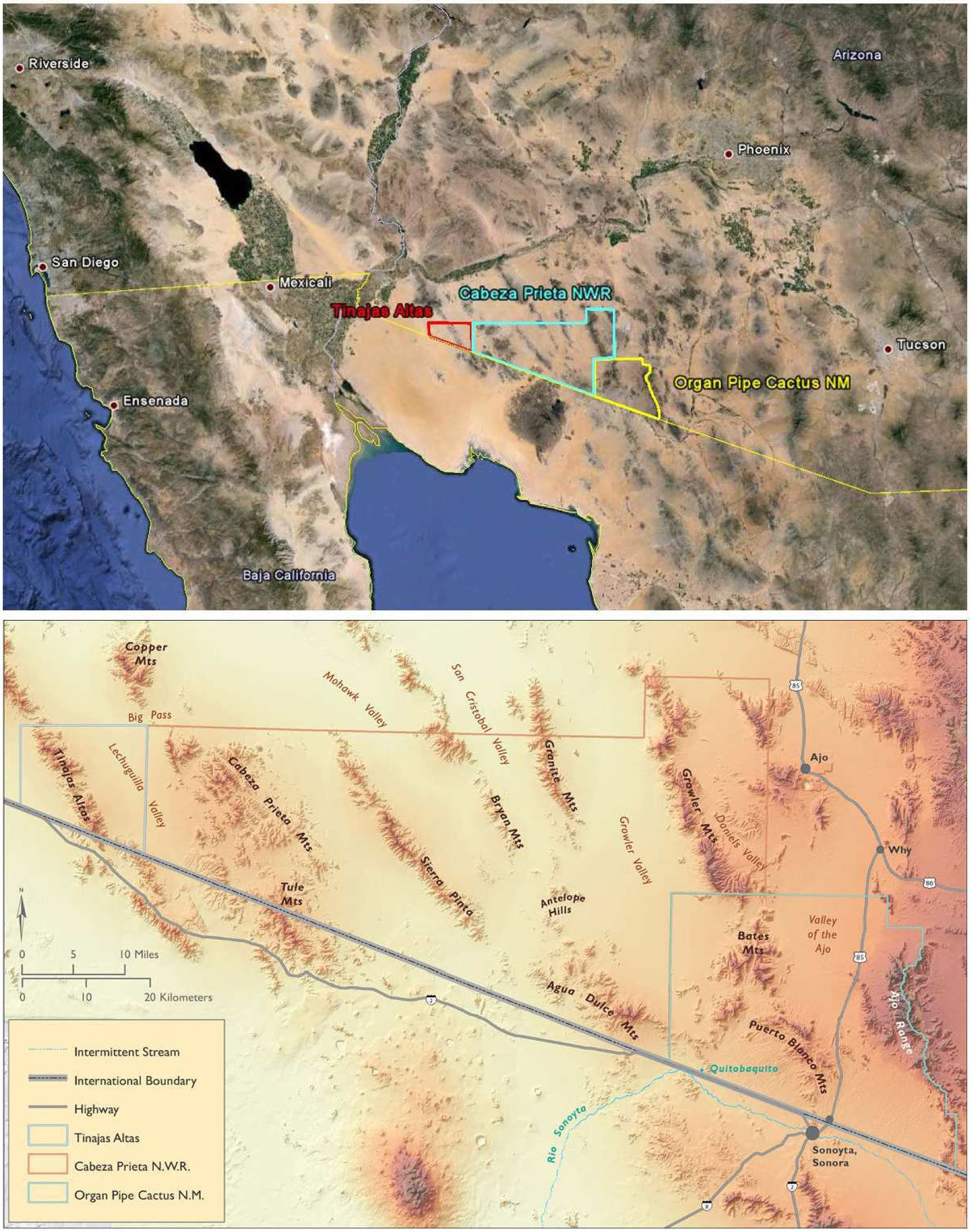

Figure 1. Flora area in southwestern Arizona. (A) Above, overview of regional context; (B) below, detail with local place names. Map B prepared by Ami Pate of Organ Pipe Cactus NM, 2013.

symbol (†). The taxa represented by fossils but no longer present in the flora area are shown with two daggers (††). Area designations are: OP = Organ Pipe Cactus National Monument, CP = Cabeza Prieta National Wildlife Refuge, TA = Tinajas Altas region. Baja California refers to the northern state and Baja California Sur to the southern state of the peninsula, and Baja California Peninsula refers to both states or when the specific state is not known. The identification keys are for the modern flora; taxa no longer occurring in the flora area are not included in the keys.

All Cactaceae are perennials and those in the Dry Borders Region (Felger & Broyles 2007) including southwestern Arizona are characterized as follows: Plants from several centimeters to tree height. Stems very succulent and spiny, or spines absent from *Opuntia basilaris* var. *basilaris*. Branches, spines, leaves, and flowers arise from highly modified short shoots called areoles; areoles on stems or floral structures often bearing extrafloral nectaries. Spines often differentiated into central and radial spines. Leaves absent, or highly reduced and soon deciduous. Flowers sessile, one per areole or multiple flowers in *Lophocereus*. Tepals (perianth segments) usually numerous and intergrading from the outer tepals (sepal-like segments) to the inner tepals (petal-like segments). Stamens numerous. Ovary inferior and deeply embedded in the receptacle, which often bears areoles, spines, scale-like bracts, or is smooth (*Mammillaria*). The proximal part of the receptacle, covering the ovary, is called the pericarpel; the distal part of the receptacle is fused to the hypanthium and the stamens on its inner surface, and is called the floral tube. The base of the floral tube forms a nectar chamber, containing sweet rewards for the pollinators. Fruits succulent or sometimes becoming dry at maturity; seeds numerous.

Nine cactus genera in our flora have extrafloral nectaries (EFNs): *Carnegiea, Cylindropuntia, Echinocactus, Ferocactus, Grusonia, Lophocereus, Opuntia, Sclerocactus,* and *Stenocereus* (e.g., Marazzi et al., unpublished manuscript; also see the species accounts, and Elias 1983 and Pemberton 1988). Whereas floral nectar rewards pollinators, extrafloral nectar rewards ants, which defend the plants aggressively from insects (herbivores) seeking young succulent morsels. The EFNs are located either on the areole "(as modified spines, or the secretory tissue embedded within spines and functional in young stages) or on floral buds (as cryptic EFNs with the secretory tissue apparently embedded within the floral bracts/scales)" (Brigitte Marazzi, pers. com. to Felger, 20 May 2014). *Echinocereus*, *Mammillaria*, and *Peniocereus* are not known to have EFNs.

In the flora area of the northern Sonoran Desert, the funnelform flowers of the two columnar cacti, *Carnegiea* and *Stenocereus*, are pollinated largely by bats, birds, and bees. The two night-blooming cereus (*Peniocereus*) are pollinated by hawk moths. The red-flowered claret-cup cactus (*Echinocereus coccineus*) is adapted for hummingbird pollination and other diurnal-flowering cacti are pollinated primarily by cactus-specialist bees. Some chollas (*Cylindropuntia*) have partially nocturnal flowers and others propagate clonally and generally have sterile flowers. Most cacti have succulent fruits adapted for animal dispersal, and relatively few have fruits that become dry at maturity. The trend for dry fruits is more prominent in the xeric, western reaches of the flora area than in the less arid eastern parts of the flora area. Seven species, or 22% of the cactus in our flora area have fruits that generally become dry at maturity or soon thereafter: *Cylindropuntia acanthocarpa, C. echinocarpa, C. ramosissima, Echinocactus polycephalus, Grusonia kunzei, G. wrightiana*, and *Opuntia basilaris*. However, the fruits of *Cylindropuntia ramosissima* and the two *Grusonia* may be facultatively semi-fleshy with favorable soil moisture.

The identification keys and descriptions pertain to plants and taxa (including genera, species and populations) occurring in the flora area and except where otherwise stated, might not cover variation of taxa or plants in other regions. All photos are by Sue Rutman unless otherwise noted.

Key to the cactus genera of southwestern Arizona

1. Columnar cacti, mature flowering plants 2+ m tall, the stems not constricted into joints or pads.

    2. Mature flowering plants usually more than 5 m tall; trunk well developed, branches none or usually arising from more than 2 m above the ground; upper (fertile) stems with 19–25 ribs.. **Carnegiea**
    2. Mature flowering plants usually not more than 5 (rarely to 7) m tall; essentially trunkless and much branched from near base; stems with 5–18 (19) ribs.

        3. Stem ribs 5–7; stems markedly dimorphic; pericarpel and fruits essentially spineless... **Lophocereus**
        3. Stem ribs (12) 15–18 (19); stems not dimorphic; pericarpel and fruits spiny (spines falling away at maturity).. **Stenocereus**

1. Not columnar cacti, mature flowering plants usually shorter than 2 m tall, or if taller (some chollas, *Cylindropuntia*) then the stems constricted into many segments or joints.

    4. Large barrel cacti, unbranched (solitary), the stem more than 20 cm diameter; larger spines stout and glabrous or with very minute non-overlapping hairs; flowers and fruits hairless .... **Ferocactus**
    4. Growth forms various, not large unbranched barrel cacti, the individual stems less than 15 cm diameter (or thick, as in some prickly-pears); spines generally not very thick and rigid (except in *Grusonia* and *Echinocactus*); flowers and fruits.

        5. Plants forming dense mounds of multiple stems ("heads") each 9–12 cm thick; spines very stout and rigid, tomentose with overlapping white hairs (use lens); exterior of flowers and fruits copiously white-woolly………………………………………………………...… **Echinocactus**
        5. Plants not forming dense mounds, the stems mostly less than 7 cm thick and the spines not exceptionally stout and rigid, or if spines stout and rigid, the plants with jointed stems; spine surfaces not covered with short hairs; flowers and fruits not woolly.

            6. Chollas and prickly-pears (opuntioids); stems constricted into joints or pads; areoles with glochids (small spines deciduous at a touch; or glochids sometimes absent in *Grusonia*) in addition to the larger persistent spines in at least some areoles (or larger spines none in *O. basilaris*); leaves present on young growth and flowers (pericarpel) but small and quickly deciduous.

                7. Prickly-pears; stem segments (cladodes or "pads") flattened or laterally compressed; surfaces relatively flat, not tuberculate; spines not sheathed……………………….. **Opuntia**
                7. Chollas; stem segments (cladodes or "joints") more or less rounded in cross-section (cylindroid), often tuberculate; spines sheathed (or the sheaths reduced and inconspicuous in *Grusonia*).

                    8. Plants often taller than wide; stems with more than 6 joints; spine sheaths covering most or all of each spine (spine sheath perhaps not evident in *C. fulgida* var. *mamillata*)……………………………………………………......…… **Cylindropuntia**
                    8. Plants usually forming colonies much wider than tall; stems with 1–6 joints; spine sheaths tiny, only at tip of spine and soon deciduous……………………...…… **Grusonia**

            6. Not chollas or prickly-pears; stems not constricted into joints or pads; areoles with or without spines but without glochids (if spines small, then not readily deciduous); leaves none.

                9. Stems less than 2 cm diameter, more than 20 times longer than wide; spines inconspicuous, 1–8 mm long, not hooked; roots tuberous; rare……………...….. **Peniocereus**

9. Stems 3–9 cm thick (if less than 3 cm then the central spines hooked), less than 10 times as long as wide; spines conspicuous, more than 8 mm long; roots not tuberous.

  10. Most areoles with at least one hooked spine; flowers (pericarpel) and fruits without scales or spines …………………………………………………………… **Mammillaria**
  10. Spines straight or curved but not hooked; flowers (pericarpel) and fruits with scales or spines.

    11. Plants usually branched, mostly from near the base, the stems more than twice as long as thick; flowers and fruits spiny………………………………… **Echinocereus**
    11. Plants usually unbranched, usually less than twice as tall as thick, ovoid to nearly globose; flowers and fruits with scales but not spineless … ……….. **Sclerocactus**

SPECIES ACCOUNTS

Carnegiea

The genus has a single species. It is the largest cactus north of Mexico.

Carnegiea gigantea (Engelmann) Britton & Rose
[*Cereus giganteus* Engelmann]
Saguaro, sahuaro; saguaro; ha:sañ. Figure 2.

Stems unbranched or mostly with several erect branches; stem tissue becoming black when cut or injured (see *Cylindropuntia fulgida* and *Lophocereus*). Stems heteromorphic, the transition from sterile (juvenile) to fertile (mature) growth and first branches often about 4–5 m above ground, the branches fertile (producing flowers). Sterile (lower) stem with 11–15+ ribs, the areoles with stout, rigid spines, the longer central spine (3.7) 5–11 cm × (0.8) 1–2.3 mm; the sterile stem portion becoming the trunk, not bearing flowers (except sometimes near the zone of transition to mature growth), often reaching more than 30 cm diameter and sometimes to 75 cm diameter (Pinkava 1995). Fertile (upper) portion of stems relatively more slender, often 35–53 cm diameter, mostly with 19–25 stem ribs, the ribs shallower than those of the sterile stems, with closely set or nearly confluent flower-bearing areoles, the spines 2–3 cm × 0.3–0.4 mm, flexible and bristle-like.

Flowers often many per rib and mostly crowded, nocturnal, opening a few hours after sunset and usually remaining open until about midday or later depending on temperature. Flowers 8.5–13 × 6.5–8 cm; receptacle narrowly funnelform, with an unusually large region of solid tissue between the ovary and nectar chamber. Larger (inner) tepals 2.3–3.5 × 1.2–1.8 cm; inner tepals, filaments, style, and stigmas white; outer tepals and scales (floral bracts) green and often with reddish tips. Areoles of floral bracts (scales) spineless or sometimes with a few bristle-like spines, and bearing small tufts of wool; floral scales bearing extrafloral nectaries. Flowering mostly late April through much of May and into early June; the first buds and flowers tend to emerge on the east side of stems; "flowers appear all over the stem apex, but are better developed on the east-facing side due to the higher temperatures there (Johnson 1924)" Drezner (2014: 587).

Fruits 6–9.5 × 3.5–4 cm just before dehiscence (opening), ellipsoid to obovoid, mostly green, sometimes red especially near the tip, spineless or sometimes with few, weak, flexible, persistent spines in some or rarely most areoles. (Stunted fruits or those developing under stress seem prone to develop spines.) Dried floral remnant often persistent (the margin of its dilated base can be used like a knife for slicing open the fruit). Fruit rind (pericarpel) bright red inside, not edible, splitting open at maturity into 3 or 4 thick, spreading to recurved lobes, and from a distance appearing like strange red flowers. Fruit pulp juicy, bright red, sweet, and delicious. Seeds about 2 mm diameter, dark red-brown to blackish, shiny and nearly smooth, and edible. Fruits mostly ripe in June and early July, rarely a few in August.

Figure 2. *Carnegiea gigantea*. (A) Near Kris Eggle Visitor Center, Organ Pipe Cactus National Monument, 4 Feb 2005. (B) Chuckwalla Hills, 19 May 2006. (C) Estes Canyon, 25 May 2005. (D) Ripe fruit, note the persistent dried floral remnant, Hwy 85 at Eagle Pass, 3 Jul 2006. (E) Lesser long-nosed bat (*Leptonycteris curasoae*) covered with *Carnegiea* pollen, Bull Pasture, 15 May 2012; the bat is held in a gloved hand to avoid potential rabies from a bite, photo by Tim Tibbitts. (F) Saguaro ribs, between Chico Shuni Village and Tepee Butte, 4 Feb 2005. (G) Cross-section of a mature stem (from a fallen plant) near Organ Pipe headquarters, 25 Jan 2005. (H) Areoles of a young plant, note the stout spines and bifurcating stem rib, Redondo Valley, north of Why, 20 Jan 2008.

Widespread and common across the region including middle and upper bajadas, hills and all mountains including the Ajo Mountains to over 4100 feet. The Puerto Blanco samples, dated at 10,500 years, are the oldest documented record for saguaros anywhere and probably reflect its arrival in the area. Some older dates for saguaro samples are contaminants (Van Devender 2002).

Sonoran Desert in Arizona and Sonora and ranging southward into thornscrub in southern Sonora, and scarcely extending into California near the Colorado River. The saguaro does not occur naturally on Baja California Peninsula.

This giant columnar cactus is the very symbol of the Sonoran Desert in Arizona and Sonora, where it a keystone species and the state flower of Arizona (e.g., Drezner 2014; Felger 2007). This genus of a single species was named by Britton and Rose, who wrote: "The genus is dedicated to Mr. Andrew Carnegie. The Desert Laboratory of the Carnegie Institution of Washington, at Tucson, Arizona, is surrounded by typical specimens of this unique plant" (1908: 188). The often repeated but unconfirmed story is that, "naming the plant for Carnegie was a ploy to extract further funding from him for plant research," but that he saw through the ploy and was not pleased (Crosswhite 1980: 6).

Saguaros are long-lived and can be truly big—over 10 m tall and up to 9000 kg (Niklas & Buchman 1994). The largest ones, however, are generally not the oldest ones. They often live about 150 years, the maximum life expectancy varying from about 125–200 years. There is considerable variation in maximum size, growth rate, and transition to adult growth (height and age of first flowering and branching), with this variation generally related to gradients in aridity and probably secondarily to local habitat differences (e.g., Drezner 2008, 2013, 2014; Drezner & Lazarus 2008; Steenbergh & Lowe 1983). For example, saguaros in the more arid, western reaches of the flora area probably live longer, commence flowering at a later age (onset of flowering may be more than a century) and generally have fewer branches and achieve smaller maximum sizes than those in the less arid eastern reaches of the flora area.

Saguaro seeds germinate with the summer monsoon (e.g., Steenbergh & Lowe 1969) and begin life in safe sites, generally beneath desert shrubs and trees, often legumes such as ironwood (*Olneya*) and palo verde (*Parkinsonia* spp.). Within the flora area, these nurse plants reduce the likelihood of a frost killing the tender young plants, by reducing heat loss to the night sky. Within the flora area but especially at the colder eastern and northern limits of the saguaro, populations are found on south-facing slopes, and often among boulders that radiate heat collected during the day. Throughout their range, nurse plants and sometimes rocks offer young plants protection from the fantastic sun of a Sonoran summer. "However, sometimes the usual nurse plants are absent, such as at MacDougal Pass and the cactus flat north of Playa Díaz—a sand flat devoid of larger desert shrubs or trees" in northwestern Sonora just south of the southeastern corner of Cabeza Prieta. "In such places *Pleuraphis rigida* [*Hilaria rigida*], a large perennial grass, is the most frequent saguaro nurse plant" (Felger 2000: 205).

The massive saguaro stems have relatively low surface-volume ratios in keeping with the need for water conservation. As with senitas (*Lophocereus schottii*) and many other large columnar cacti, the younger plants have fewer stem ribs, resulting in a lower s/v ratio, while the fertile stems of the larger plants have more stem ribs and a higher s/v ratio (Felger & Henrickson 1997). Cross-section outlines for two sample saguaro fertile stems, 35 and 53 cm diameter, are shown in figure 35. Both stems have 22 ribs and low s/v ratios, ranging from 0.1–0.17 cm^2 per unit volume. The ratios were determined from cross sections. If each stem were a true cylinder, with these diameters the s/v ratios would be smaller still, about 0.07–0.11 cm^2 per unit volume. When these values are compared to the measured s/v ratios, one can see that the ribs have only a minor effect on the s/v ratio in this large-stemmed cactus. This favorable s/v ratio for water conservation is achieved at the expense of limiting photosynthetic tissue and replacing it with large volumes of non-photosynthetic, water-storing tissue (Drezner 2003; Mauseth 2000; also see discussion for *Peniocereus striatus*).

The abundant flowers and fruits of the saguaro are irresistible to the Sonoran Desert fauna. The lesser long-nosed bat (*Leptonycteris yerbabuenae*) is among the important pollinators and seed dispersers at night along with the western white-winged dove (*Zenaida asiatica mearnsii*) in daytime (e.g., Fleming 2002; Fleming et al. 1996; Martínez del Rio 2007). Numerous other birds, bees and other insects, also visit the flowers, as well as small mammals like round-tailed and Harris antelope ground squirrels (Tim Tibbitts, observation; also see *Stenocereus thurberi*). The fruits are consumed and seeds dispersed by an even wider range of animals, including coyotes, javelinas, lizards, desert tortoises, and birds ranging from ravens to cactus wrens, finches, and orioles. The lesser long-nosed bats feed on floral nectar of saguaros as well as that of organ pipes and agaves (*Agave palmeri*). The agave pollen is large-grained, sticky, and a rich yellow color, imparting a golden-yellow color to the bat's fur. Saguaro pollen by comparison is finer, drier, and paler, imparting a pale blonde color to the bat's fur. However, the saguaro doesn't enjoy a commensal relationship with all its neighbors. Saguaros are sometimes uncommon near waterholes, especially in the Tinajas Altas region, undoubtedly due to the desert bighorn that smash the stems with their horns in order to eat the succulent tissue (Felger et al. 2012; Russo 1956).

The ecologist Forrest Shreve observed, "The sahuaro appears to suffer from very few diseases and natural enemies, the greatest decimation in its numbers being occasioned by mechanical agencies. When struck by lightning or wounded in any other manner during the dry season, it recovers rapidly by the formation of a heavy callus over the wounded spot. If it is wounded in the rainy season, however, bacterial decay sets in very rapidly and a large plant may be destroyed in less than a week as a result of a small wound." (Shreve 1920: 166). Shreve was correct concerning recovery from most dry-season wounds but more hopeful than accurate on the recovery from lightning, which in any case would rarely occur during the dry season. For instance, on 4 September 1969, following a spectacular storm in the Tucson Mountains of Saguaro National Park, Warren Steenbergh surveyed 17.7 ha and found 11 victims of "instant death by explosive mechanical breakage and massive destruction of cell tissues" (Steenbergh 1972). An ongoing study of about 135 reproductive individuals on a 0.96 ha plot adjacent to Saguaro National Park (East) recorded death-by-lightening for three individuals between 1997 and 2014 (William Peachey, pers. comm. to Malusa 2014). Victims are inevitably among the largest individuals—the lightning rods of the desert.

The hot bolts of the summer monsoon are not the only violent agent of mortality for the giant cactus. Blowdown can occur whenever these large, heavy plants are turgid and the soil is wet and relatively soft. At least 60 large saguaros were blown over in a microburst wind and rainstorm one night in August 1992 in the vicinity of Little Tule Well, visible from the road along a distance of about 2 km, and the area of wind-felled giant cacti extended far beyond those two kilometers. Nearly all these saguaros were lying in the same direction with the tips pointing southwest. In addition many large chollas (*Cylindropuntia fulgida* and some *C. bigelovii*) and a few large ocotillos (*Fouquieria splendens*) had blown over. For severe weather events, the winter storm of January 21–22, 2010 was noteworthy. Within view along the South Puerto Blanco Drive, 156 saguaros, 3 organ pipes, and 1 senita cactus fell over as a result of this storm. All except one saguaro were large individuals. Maximum wind speed at the nearby town of Ajo reached 94 mph on January 21 (Bohlin et al. 2010); in the previous 24 hours, 2.5 inches of rain had fallen at the nearby Senita Basin weather station (Organ Pipe Cactus National Monument 2011). A combination of high wind and wet soil was responsible for this blowdown event; higher gusts have been recorded in previous years when the soil was not as wet, without any blowdowns of this magnitude.

The saguaro is the most culturally important and revered plant in the flora region and across the Sonoran Desert in Arizona and northern Sonora (Bell et al. 1980; Booth 2005; Bruhn 1971; Castetter & Bell 1937; Castetter & Underhill 1935; Crosswhite 1980; Felger et al. 1992; Hodgson 2001; Lumholtz 1912; Nabhan 1982, 1985; Nabhan et al. 1982; Rea 1997; Toupal 2006; Betty Melvin in Zepeda 1985: 73). The fruit, ripe in early summer, served as a major food resource, and people seasonally moved their residences for the harvest. Important saguaro fruit-gathering camps for the Hia C'ed O'odham included Ajo, Bates Well, the Quijotoa Mountains, Quitovac, and Santa Rosa (Bell et al. 1980), and some camps were used for harvesting organ pipe fruit as well (Hodgson 2001). The Presidential Proclamation establishing Organ Pipe Cactus National Monument in 1937 specifically allows the O'odham to continue their traditional harvesting of the fruits.

The juicy, sweet pulp is eaten fresh, dried for later use (see organ pipe, *Stenocereus thurberi*), or made into syrup and wine. The protein- and oil-rich seeds are ground and consumed, either freshly harvested or stored. Saguaro and organ pipe wine is ceremonially important among O'odham groups in the Dry Borders region. "They eat [saguaro fruit] and they eat the syrup out of the [saguaro fruit] and jam. . . and seeds. . . they [make gruel with wheat]" (Betty Melvin in Zepeda 1985: 73). Lumholtz (1912: 331) mentioned that Hia Ced O'odham "used to come as far as Quitovaquito and Santo Domingo to gather mezquite beans. . . and eat sahuaro and pitahaya." (Santo Domingo was an hacienda near Quitobaquito along the Río Sonoyta.)

The term *pitahaya* has been used to refer to columnar cacti in general, including the saguaro and organ pipe, as well as *Echinocereus* (Castetter & Underhill 1935; Crosswhite 1980; Felger 2007; Mitch 1972). The 17th century travels of Kino and Manje must have been sustained in part by the dried fruits, for they rarely traveled during the summer yet often mention the pitahaya fruits given to them by the people of Pimería Alta (Burrus 1971). When ripe saguaro fruits open, the red seed-filled pulp may fall from the husk (pericarpel) to dry in branches of nurse trees or on rocky ground. These have been gathered by Tohono O'odham as a sweet treat called *chuñ.* Saguaro fruit dried as fruit leather can be kept for many months, eaten as nutritious trail food, or pressed like figs in "saguaro newton" cookies (Martha Ames Burgess, pers. com. to Felger, 2014; also see Hodgson 2001).

The dry, woody stem ribs were used for construction material—made into slats for house frames, walls, and shelves, and also fashioned into saguaro fruit-gathering poles, light tools, tongs for picking cholla buds and joints, cradleboards, bird cages, traps for quail, and fire drill boards (Bell et al. 1980; Felger 2007; Felger et al. 1992). Cactus "boots," the woody calluses formed around woodpecker or flicker holes, were fashioned into various containers or vessels, including drinking bottles, dishes, and tobacco pouches. Ezell (1937) and Haury (1938/1965) deduced that the Hohokam used vinegar from saguaro wine to etch designs on seashells that are so abundant in the archaeological record.

OP: South Puerto Blanco Drive, 6 km W of Hwy 85, 26 Apr 1990, *Felger 90-70* (ARIZ, ORPI 15309). Upper bajada of Ajo Mts along Alamo Canyon Road, *Rutman 12 Jun 2002* (ORPI 14849). Senita Basin, *Anderson 14 Jun 2002* (ORPI 14848). †Alamo Canyon, seeds, 8130 & 8590 ybp. †Puerto Blanco Mts, on ridge, seeds, from modern (30) to 10,540 ybp (20 samples).

CP: Charlie Bell Road near the E Refuge Boundary, 12 Jun 1992, *Felger 92-532*. 3.1 mi W of Tule Well on Camino del Diablo, 5 Mar 1995, *Rebman 2884* (DES).

TA: See Felger et al. (2012). †Tinajas Altas, seeds, 1230 to 8970 ybp (6 samples). †Butler Mts, seeds, 3820 to 10,500 ybp (4 samples; also to 11,250 ybp, but dates older than 10,500 years may be contaminants).

Cylindropuntia – Cholla; *choya*

Low-growing to shrub-sized cacti (or sometimes small trees). Stem segments (joints or cladodes) cylindrical and longer than wide. Spines uniquely enveloped with a deciduous epidermal sheath. Spine glands as nectaries in the upper part of areoles functioning on young stems, floral buds, and flowers. Flowers diurnal, except crepuscular or nocturnal in *C. fulgida* and *C. leptocaulis*, and *C.*

ramosissima. The genus includes 35 species native in western USA, Mexico, and the West Indies. The greatest diversity is in southwestern USA and adjacent Mexico, and especially the Sonoran Desert region.

The three opuntioid genera (subfamily Opuntioideae) in the flora area, *Cylindropuntia* (chollas), *Grusonia* (club chollas), and *Opuntia* (prickly-pears), are generally characterized as follows: Stems with determinate, rhythmic (seasonal or annual), constricted growth increments resulting in individual stem segments or cladodes (called "joints" in chollas and club chollas, and "pads" in prickly-pears). Areoles bear glochids (small, readily detachable spines with tiny retrorse barbs), and at least some areoles bear spines, which generally are not readily detachable (spines absent on *Opuntia basilaris* var. *basilaris*). Young, growing stem segments and buds and flowers bear small but conspicuous leaves, 1 per areole, succulent, subulate, cylindrical, or conical, and are soon deciduous. These small, vestigial leaves have C_3 photosynthesis, in contrast the rest of the plant and most cacti (including those in the flora area), which have CAM photosynthesis. The stamens are sensitive: the filaments close inward when touched, for example enveloping a pollinating bee. The actual seeds are enclosed in larger, light tan, bony aril-like structures, which look like seeds. This bony aril-like covering of opuntioid seeds forms as flaps along the margins of the curled distal part of the funiculus. The actual seed has a nearly smooth, dark brown testa (seed coat) and a shape much like that of other large cactus seeds, but is fused to the inner surface of the much larger and variously shaped aril-like cover.

Cylindropuntia, with 12 taxa in the floral area, is the most diverse cactus genus in the region as well as in the Sonoran and Chihuahuan Deserts. Chollas are a conspicuous feature of the landscape across the flora area. The chollas of the eastern, or Arizona Upland areas of the flora area have fleshy fruits (except *C. acanthocarpa*), while the "western" species, in the more arid Lower Colorado Desert region, tend to have fruits that quickly become dry upon ripening.

Sue Rutman found many cholla populations significantly reduced during the deep drought in the decade beginning in the early 2000s, including widespread die-off in Organ Pipe and Cabeza Prieta and southward in northwestern Sonora. Not only was the drought significant enough to cause loss of turgidity and mortality, but also small mammals began eating chollas for scarce moisture. The smaller chollas with relatively high surface/volume ratios, such as *C. leptocaulis* and *C. ramosissima*, experienced the greatest die-off. For example, near Teepee Butte in Cabeza Prieta, only a small percentage of *C. ramosissima* remained by about 2010 in an area where the species previously was a major part of the landscape. As of 2014, these populations had not recovered. Similar drought-induced die-off of chollas has been documented in other regions of the Sonoran Desert (Bobich et al. 2014).

Ranchers occasionally burn the spines off both chollas and prickly-pears to make them more palatable for cattle, a process referred to as *chamuscando* (scorching the exterior), which dates back to mid-1700s. For example, Ratcliff (1946) reported that in Organ Pipe, "The Grays have burned cholla cactus to furnish some food for the stock. After the spines have been burned off the cattle eat all edible portions down to the stalk."

Flower buds and young cladodes (joints or stem segments) of the larger chollas were harvested in spring and cooked as vegetables. The fruits of the fleshy or succulent-fruited species were eaten fresh or cooked. The large "seeds" were discarded. The spines and glochids of chollas and prickly-pears were removed by several methods including vigorously brushing them in sand or gravel, often using a creosotebush (*Larrea*) branch as a brush, or soaking in water (e.g., Childs 1954; Felger 2007; Felger & Moser 1985; Hodgson 2001; Rea 1997).

1. Fruits proliferating in perennial pendant chains, not spiny, remaining green and fleshy when ripe, present all year .... **Cylindropuntia fulgida**
1. Fruits single, not proliferating in pendent chains (occasionally with 2 fruits together), the fruits fleshy and green or yellow, present all year or less, spiny or not, and sometimes becoming dry upon ripening.

  2. Main axis (trunk) well developed, generally straight and erect; fruits yellow.

    3. Joints (3) 4–6+ cm diameter (excluding spines), and very readily detachable; stem surfaces obscured by a dense cover of spines; inner tepals pale yellow-green; fruits soon becoming dry or sometimes persisting and semi-fleshy .... **Cylindropuntia bigelovii**
    3. Joints less than 3 cm diameter, not readily detachable; stem surfaces generally visible; inner tepals fuchsia to purple; fruits fleshy and persistent. .... **Cylindropuntia spinosior**

  2. Main axis (trunk) not well developed, or if so, then usually not straight and erect; fruits generally not yellow.

    4. Joints 1.5 cm or more in diameter, the surfaces visible through a sparse cover of spines or partially to fully obscured by spines, each joint usually evenly spiny from the base to the tip; stems variously purplish, reddish, or greenish.

      5. Fruits remaining fleshy at maturity and semi-persistent .... **Cylindropuntia versicolor**
      5. Fruits dry when mature and not persistent.

        6. Stem tubercles mostly 16–24 mm long; inner tepals variable—yellow, orange-brown to dull golden-yellow, red, or purple, the filaments red or red-purple (occasionally green); basal tubercles of fruits much longer than upper tubercles .. **Cylindropuntia acanthocarpa**
        6. Stem tubercles 11–16 mm long; inner tepals green; filaments green to yellow; basal tubercles of fruits nearly equal to the upper ones .... **Cylindropuntia echinocarpa**

    4. Joints mostly 1 (1.2) cm or less in diameter, the surfaces readily visible through a sparse cover of spines, the lower areoles of each joint likely to bear only glochids; stems remaining green all year.

      7. Tubercles rather flat but sharply defined with diamond-shaped (rhomboid) outlines; each areole in a groove; fruits dry and bristly at maturity.................... **Cylindropuntia ramosissima**
      7. Tubercles relatively obscure or poorly developed, the stem surfaces smooth; areoles not in grooves; fruits fleshy and not bristly at maturity.

        8. Plants usually with a short but thick, woody trunk; terminal joints mostly 7–12 mm diameter; ripe fruits yellow-green or mostly green (sometimes tinged with pink or pale red) .... **Cylindropuntia arbuscula**
        8. Plants without a well-defined trunk; joints mostly 4.5–6.5 mm diameter; ripe fruits bright red-orange .... **Cylindropuntia leptocaulis**

Cylindropuntia acanthocarpa (Engelmann & J.M. Bigelow) F.M. Knuth
[*Opuntia acanthocarpa* Engelmann & J.M. Bigelow, 1856]
Buckhorn cholla; *choya*; ciolim (also called hanamĭ, the general term for cholla). Figures 3 & 4.

Shrubby chollas, 0.4–2 m tall; trunk often poorly defined, not straight; branching at various heights, the branches including the ultimate joints upright to spreading, green to grayish green, and becoming reddish purple on some plants in winter and dry seasons, while other plants, even adjacent ones, remain green or greenish. Stem segments (joints) firmly attached. Mid-joint stem tubercles 1.5–3 cm long, more than twice as long as broad. Spines moderately to quite densely covering the joints, often partially obscuring stem surfaces; spines highly variable among individual plants, even adjacent ones: spines white, yellow to dark grayish or reddish purple, the spine sheaths yellow and inflated (baggy) to dark in color and tightly fitting (not baggy). Flowers 5–6 cm wide, highly variable in color but uniform on an individual plant: inner tepals uniformly dull to bright yellow, golden-yellow, orange or orange-brown, red–orange or reddish, rose-pink, or sometimes bright red; flowering April and May. Filaments red, or rarely green; anthers yellow. Fruits dry after ripening, generally within one to several months, bur-like with bristly spines, and not persistent, the basal tubercles of fruits much longer than upper tubercles; dry fruits variously tan to purplish black, eventually becoming gray or brownish, or fruits sometimes infertile, tan, and shriveled.

Buckhorn cholla is common and widespread across most of the flora area; sandy to rocky soils on hills and mountains, bajadas, and desert plains and valley flats, from the lowest elevations to the higher mountains. It has been part of the local flora for at least 20,500 years.

Cylindropuntia acanthocarpa occurs in the Sonoran and Mohave Deserts: northwestern Sonora, western and central Arizona, southeastern California, southern Nevada, and southwestern Utah. Populations in northwestern Baja California formerly included in C. *acanthocarp*a have been segregated as *C. sanfelipensis* (Rebman) Rebman. *Cylindropuntia acanthocarpa* is diploid and has bisexual (perfect) flowers, while *C. sanfelipensis* is hexaploid and gynodioecious (Rebman 1995, 1999). There are, however, other gynodioecious chollas.

The flower buds and young stems (cladodes or joints), harvested in spring and often pit-baked, have been important food resource for O'odham people since prehistoric times (Felger 2007; Greenhouse et al. 1981; Hodgson 2001). Seepweed (*Suaeda nigra*) often was used to line the pit and as the interlayered steamer (Curtin 1949; Rea 1997; Russell 1908), or saltbush (*Atriplex* spp., including *A. cansescens*) was used if seepweed was not available (Martha Ames Burgess, pers. comm. to Felger, 2014). Betty Melvin (in Zepeda 1985: 55) related that the Hia Ced O'odham "collected the cholla buds, we'd collect it and dry it." The baked, dried flower buds continue to be a favored food of the regional O'odham people (Hodgson 2001; Rea 1997) and are available in southern Arizona as a gourmet specialty food (Burgess 2014).

Four intergrading varieties *Cylindropuntia acanthocarpa* have been recognized by Benson (1982) and Pinkava (1999a, 2003a), two of which occur in the flora area. Chollas in the flora area called variety *coloradensis* are reported as generally replacing those called var. *major* westward in the Lower Colorado Valley area, encompassing portions of the western part of Organ Pipe and most of Cabeza Prieta and the Tinajas Altas region. Variety *coloradensis* is characterized by yellow or yellowish spines and spine sheaths, with the sheaths more inflated and the plants more robust and with a more upright growth habit than in var. *major.* Recent data collected by Baker suggests that var. coloradensis should be included within var. acanthocarpa.

Chollas in the flora called var. *major* are reported as primarily occurring in Arizona Upland areas including higher elevations in the flora area encompassing most of Organ Pipe and the eastern part of Cabeza Prieta. Variety *major* has been identified as having spines yellowish to commonly dark with dark and tightly fitting (not baggy) spine sheaths, and the plants generally being less robust and with branches more often spreading, and the joints shorter and not as densely spiny as var. *coloradensis*. These distinctions, however, are often feeble and plants identifiable as either variety can be found across the flora area, including plants next to each other. Another problem involves the neotype locality of var. *major* in Organ Pipe, which is confusingly situated in or near the zone of reported intergradation; thus the epithet *major* has been used for the eastern populations more or less by convention (Felger & Zimmerman 2000).

According to Prof. Donald Pinkava (1999a), populations of *Cylindropuntia acanthocarpa* var. *thornberi* (Thornber & Bonker) Backeberg occur in northwestern Arizona. Variety *acanthocarpa* does not occur in the Sonoran Desert but var. *thornberi* does, just north of Phoenix at Table Mesa and in the Horseshoe Dam area. Marc Baker's research suggests that populations of var. *thornberi* are restricted to higher elevations east of those of var. *acanthocarpa* and north of those of var. *major*. In either case, the varieties *acanthocarpa* and *thornberi* are not entirely geographically or morphologically segregated. For example, Prof. Pinkava identified several specimens at ASU collected from the original type locality of *C. acanthocarpa* at Cactus Pass, Yavapai County as var. *thornberi* and specimens from the lectotype locality of *C. acanthocarpa* at Hillside, Yavapai County (see Benson 1982: 913) as approaching var. *thornberi*.

Since Benson (1969: 20) did not find the type specimen of *Opuntia echinocarpa* var. *major* Engelmann & J.M. Bigelow (*C. acanthocarpa* var. *major*) from the collection of Arthur Schott in 1855 (Engelmann & Bigelow 1856), he designated a neotype at the herbarium of Pomona College (POM) and reported a "Duplicate: Herbarium of the Organ Pipe Cactus National Monument." The neotype is indeed at the POM herbarium (incorporated into RSA) but no duplicate (it would be an isoneotype) was found at the Organ Pipe herbarium (ORPI) and it probably never was there. Steve Boyd at RSA (pers. comm. to Felger, 2005) wrote, "I feel like you were pretty lucky on this one. Benson's cacti were not well curated, with lots of things, including many he cited as neotypes, lacking determinations. I wouldn't be surprised if Benson never deposited the other specimen at Organ Pipe, based on what I've seen of his material, processed and unprocessed."

Cylindropuntia acanthocarpa might be confused with *C. echinocarpa*, and both are members of subgenus *Cylindropuntia*. In general *C. acanthocarpa* forms larger and more openly-branched plants and *C. echinocarpa* is more densely branched and more densely spiny with whiter spines, the plants are often smaller, and generally occur in drier, hotter areas, although their geographic ranges overlap. The fruit umbilicus (depression of flower scar on fruits) is usually shallow in *C. acanthocarpa*. "Seeds" (the seed enclosed in the bony aril) of the two species, at least among specimens from the flora area, are remarkably similar. In both species the developing seeds form facets or angles where they press against one another tightly packed in the developing fruit (the fruits lack a succulent matrix that might keep the developing seeds apart). Yet the seeds of *C. echinocarpa* are often somewhat smoother, with few angles or facets, and more nearly disk-shaped than those of *C. acanthocarpa*; and perhaps *C. echinocarpa* has fewer seeds per fruit than *C. acanthocarpa*. The differences, however, do not seem reliable enough to use as key characters. A difference in length of stem tubercles, however, is a reliable key feature that can be seen at any time of year. To add to the confusion, however, hybrids between the two species occur frequently in areas of sympatry. The putative hybrid, *C. ×deserta* (Griffiths) Pinkava, is morphologically intermediate and often bears flowers with intermediate coloration. Backcrossing may lead to the introduction of introgressant characters in otherwise typical individuals of either parent. Within the flora area there is a general trend for *C. echinocarpa* to more often occur in valleys and sandy soils, and *C. acanthocarpa* to be prominent on rocky slopes, even to peak elevations, and both can be common on bajadas.

Although the biological reality of the two varieties of *C. acanthocarpa* in southwestern Arizona can be problematic, they are reported to be distinguished as follows:

1. Plants branching at or near the base, branches mostly erect or ascending; sparsely branched; tubercles mostly greater than 6 mm wide and 6 mm high; spines ca. 18 per areole, the spine sheaths bright white or pale yellow, mostly absent after the first or second year; unsheathed spines dull yellow

or flesh colored or sometimes brown (on melanistic forms); sheathed central spines conspicuously wider (mostly more than 1 mm thick) and longer than auxiliary central spines and radials; contrast between the color of the new joints with sheathed spines and old joints with unsheathed spines is striking. .... **Cylindropuntia acanthocarpa** var. **coloradensis**

1. Plants with a single stem or several stems from the base, erect or spreading; densely branched; tubercles mostly less than 5 mm wide and less than 6 mm high; spines ca. 12 per areole, the unsheathed spines bright pale yellow or whitish, brown, rust or grey and sometimes multi-colored; sheathed central spines not much thicker than 0.5 mm and not conspicuously wider than auxiliary central or radial spines.. **Cylindropuntia acanthocarpa** var. **major**

Figure 3. *Cylindropuntia acanthocarpa* var. *coloradensis.* (A & D) Kofa Queen Canyon, Kofa Mts, 5 Apr 2014: (D) note spine sheaths drop off after 1–2 years, revealing dull, beige-colored spines. (B & C) Near Horse Tanks, Castle Dome Mts, 6 Apr 2014: (B) note central spines distinctively larger than radial spines and sheaths whitish, reflective, and baggy.

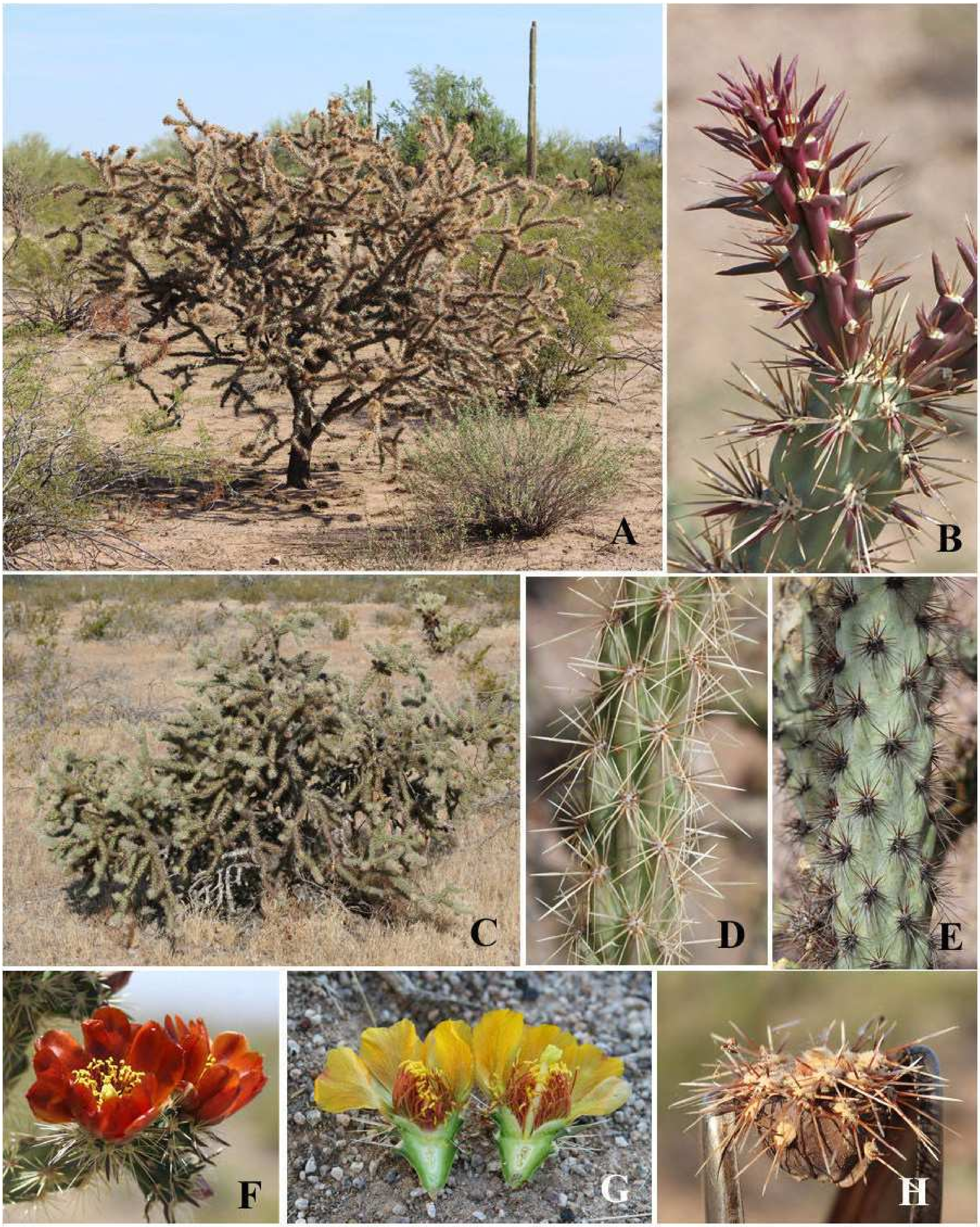

Figure 4. *Cylindropuntia acanthocarpa* var. *major*. Valley of the Ajo, near intersection of Hwy 85 and Armenta Ranch Road: (A) 3 Jul 2013; (H) fresh, nearly dry fruit (held in tongs), 17 Jul 2013. (B) Developing stem with leaves, Ajo Mountain Drive, W of Ajo Mts, 2 Aug 2013. Alamo Wash, 1 mi E of Hwy 85: (C, D, E) 17 Jul 2013; (G) 23 May 2006. (F) Near N boundary of OP, E of Hwy 85, 12 May 2006.

Cylindropuntia acanthocarpa var. **coloradensis** (L.D. Benson) Pinkava
[*Opuntia acanthocarpa* var. *coloradensis* L.D. Benson]. Figure 3.

OP: 1 km NNE of Red Tanks Well, 2000 ft, 4 Mar 1988, *Baker 7578* (ASU, ORPI 9771). 2 km NW of Dripping Springs, 525 m, 7 Mar 1988, *Baker 7587* (ASU, ORPI 8891). 0.8 km E of summit of Twin Peaks, 1740 ft, collected because of the odd flowering time, flowers brown-orange, 1 Aug 1990, *Baker 7883* (ORPI 9793). 2 km W of Hwy 85 at N boundary of Monument, [including] *C. leptocaulis, Ferocactus emoryi, Mammillaria grahamii, Opuntia engelmannii, O. fulgida var. fulgida, Peniocereus greggii*, 2 Dec 1990, *Felger 90-501* (both yellow-spined and dark-spined plants present). Granite hills, Gunsight Hills, E of Kuakatch, with *Larrea, Opuntia fulgida, O. leptocaulis, O. arbuscula, O. phaeacantha*, 14 Mar 2003, *Rutman 2003-533* (ORPI 14850). Mouth of Alamo Canyon, *Rutman 14 Apr 2003* (ORPI). Trail from The Cones to Mount Ajo, 4090 ft, 10 Apr 2005, *Felger* (observation).

CP: 7 mi E of Papago Well, 14 Mar 1937, *Harbison 17004 & 17005* (SD). 3.1 mi W of intersection at Tule Well along Camino del Diablo, flowers golden-yellow with outer tepals showing some magenta, filaments red, anthers yellow, style cream, stigma cream-green, 5 Mar 1995, *Rebman 2883* (ASU, SD).

TA: E end of Tinajas Altas Pass, 12 Feb 1977, *Reeves R5395* (ASU). Mesa 1 km E of Tinajas Altas, 22 Nov 2008, *Felger 08-190*. Flats adjacent to granitic hills, SW side of Tinajas Altas range, 10 Jan 2002, *Felger* (observation).

Cylindropuntia acanthocarpa var. **major** (Engelmann & J.M. Bigelow) Pinkava
[*Opuntia echinocarpa* Engelmann var. *major* Engelmann & J.M. Bigelow, Proc. Amer. Acad. Arts 3: 305–306, 1856. *O. acanthocarpa* var. *major* (Engelmann & J.M. Bigelow) L.D. Benson]. Figure 4.

OP: Headquarters of the Organ Pipe Cactus National Monument, 2500 ft, sandy soil, 26 May 1962, *Steenbergh 5-2662-1* (neotype of *Opuntia echinocarpa* var. *major* Engelmann & J.M. Bigelow, POM 306088/RSA).

Variety not designated:

OP: Quitovaquito, 28 Nov 1939, *Harbison 26185 & 26192* (SD). Growler Well, *Nichol 27 Apr 1939* (ORPI 1154, det. Lyman Benson 1962). Aguajita Wash, 6 Apr 1988, *Felger 88-323*. 2.4 mi W of Hwy 85 on Puerto Blanco Drive, 19 Jun 1989, *Felger 89-225*. †Alamo Canyon, seeds, 1150 to 17,830 ybp (4 samples). †Montezuma's Head, seeds, 20,490 ybp. †Puerto Blanco Mts, on ridge, seeds, 980 to 9720 ybp (12 samples).

CP: Observations, *Felger*: Agua Dulce Pass, Eagle Tank, Buckhorn Tank, Cabeza Prieta Tanks, 13–15 Jun 1992; Childs Mt, 2845 ft, 18 Aug 1992.

TA: †Tinajas Altas, seeds, 1230 to 10,070 ybp (6 samples).

Cylindropuntia acanthocarpa × C. spinosior

There are two herbarium records for this putative hybrid in Organ Pipe. Sue Rutman found additional plants in the north-central part of Organ Pipe about two miles from the nearest known *C. spinosior*. Fruits of the hybrid are yellow, spiny, and dry earlier than those of *C. spinosior* but later than those of *C. acanthocarpa*. *Cylindropuntia acanthocarpa* has dry, spiny fruits and *C. spinosior* has fleshy yellow, and spineless fruits.

OP: W of Bates Mts, plants to 2 m tall, with *Opuntia arbuscula, O. leptocaulis*, *O. fulgida*, etc., 23 Mar 1990, *Baker 7774* (ASU). Just across international border from Las Palmas, 1410 ft, just S of Dos Lomitas, UTM: 12 334300 3526300, *Atriplex polycarpa* flats with *Larrea*, *Opuntia fulgida, O. leptocaulis, Peniocereus greggii, Prosopis glandulosa*, shrub 1.8 m tall, flowers red-purple, style pale red-purple above, pale green-yellow below, stigma cream-white, fruits pale green and/or yellow, often tinged with red-purple, especially about areoles, 23 May 1991, *Baker 8366* (ASU, SD).

Cylindropuntia arbuscula (Engelmann) F.M. Knuth
[*Opuntia arbuscula* Engelmann]
Pencil cholla; *siviri, tasajo*; vipinoi. Figure 5.

Shrubby chollas, 0.8–2+ m tall, sometimes with a thick woody trunk, much branched above, with a dense crown. Smaller (ultimate) joints readily detaching, mostly (3.5) 4–15 cm × (7) 8.5–12 mm, green to yellow-green all year; tubercles scarcely raised; areoles rather widely spaced; spines 1.8–3.5 cm long, slender, mostly one spine per areole, less often 2 or 3, the lower areoles on each joint mostly spineless. Flowers 2–3.5 cm wide; inner tepals greenish yellow, yellow, or yellow-brown; outer tepals reddish, purple, or orange; filaments green; anthers yellow. Fruits fleshy, often produced in large quantities and 1 or often several fruits at a stem tip, often persistent for about 1 year, 2.3–2.8 cm × 10.7–12 mm, sometimes enlarging with age, yellow-green or green even when ripe, or sometimes with slight reddish or yellowish tinge, the umbilicus (the top the fruit) unusually deep. Flowering April and early May. 2*n* = 66.

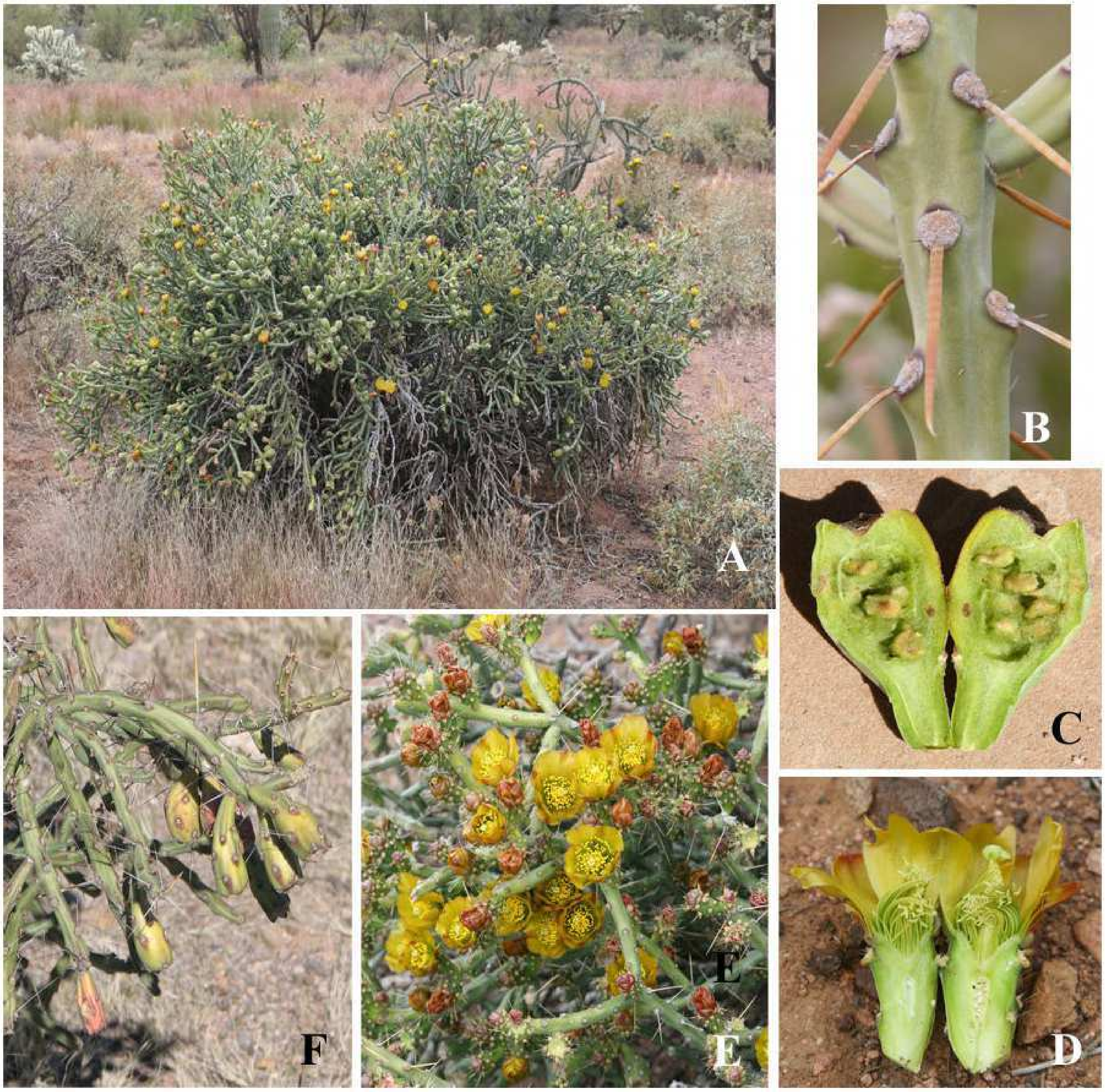

Figure 5. *Cylindropuntia arbuscula*. (A, D, & E) Ajo, 30 Apr 2005. Sandy plain near Kuakatch Wash west of Hwy 85: (B) portion of stem, 4 Mar 2009; (C) fruit, 28 Feb 2008. (F) Redondo Valley, N of Why, 20 Jan 2008.

Widely scattered in Organ Pipe, mostly in sandy loam soils of valley bottoms and bajada plains, and sometimes along the margins of arroyos. Also at the eastern extent of Cabeza Prieta between the Growler Mountains and Daniel's Arroyo, where this cholla thrives in narrow gullies cut into caliche terraces. This cholla does not range farther westward from the flora area.

Arizona from Maricopa County southward and Sonora southward to the coastal plain southeast of Guaymas.

Cylindropuntia arbuscula is hexaploid, 2*n* = 66 (e.g., Pinkava 2003a). Pentaploid chollas, which often form local clones, have been called *C. arbuscula* (Pinkava 1999a) but are probably hybrids with *C. arbuscula* as a parent or are hybrids with a different origin than *C. arbuscula* (*C. arbuscula* is likely of hybrid origin with *C. leptocaulis* as one of its parents). Marc Baker determined chromosome numbers of *C. arbuscula* from various locations in Pima County and elsewhere and concludes that most individuals of true *C. arbuscula* (2*n* = 66) generally bear only a single spine per areole on mature stems and sporadically two or three spines per areole. The pentaploids, which include the clonal microspecies *C.* ×*neoarbuscula* F.M. Kunth and *C.* ×*vivipara* F.M. Kunth and probably a few other unnamed clones of hybrid origin, all generally bear three or more spines per areole on mature stems.

Gila River Pimas cooked the buds and fruit in the same manner as those of *C. acanthocarpa*, but *C. arbuscula* fruits were said to taste different, being a bit more sour (tart) than those of *C. acanthocarpa*. Pencil cholla buds and fruits were often dried for future use (Rea 1997). O'odham plant expert, Juanita Ahil (1915–1994) preferred pencil cholla buds and fruits when she could find them, rather than those of other chollas (Martha Ames Burgess, pers. comm. to Felger, 2014). The fleshy fruits are eaten fresh by the Seris (Felger & Moser 1985).

OP: Senita Basin, 23 Mar 1969, *Lehto 15428* (ASC). Growler Canyon, 1400 ft, 19 Oct 1987, *Baker 7573* (ASU, ORPI 8887). 1 mi W of Hwy 85 on Kuakatch Wash Road, 24 Jul 1978, *Bowers 1381* (ORPI 1982). Rocky slope 0.5 km N of Aguajita Spring, 6 Apr 1988, *Felger 88-321*. Hocker Well, 3 Dec 1990, *Felger* (observation).

CP: 2 km SW of Cameron's Tank, 1650 ft, UTM (Zone 12N) 317400 E, 3568250 N (NAD 1927), *Malusa* (observation), 8 Feb 2000.

Cylindropuntia bigelovii (Engelmann) F.M. Knuth
[*Opuntia bigelovii* Engelmann]
Teddybear cholla, jumping cholla; *choya güera*; hadsadkam (also called hanamĭ, the general term for cholla). Figure 6.

Chollas often 0.5–1.8 (2) m tall, the trunk erect, stout, straight, and beset with dead, persistent branches (joints) with blackened spines. As with many chollas, the root system is a cluster of fibrous roots with a few horizontal lateral roots of indeterminate lengths. Joints relatively short and thick, and readily detaching, green all year, with extrafloral nectaries (areolar glands) green when fresh, seen on the new growth. Spines dull yellow and densely covering and obscuring the stems segments (joints), and with prominent yellowish spine sheaths. Flowers yellow-green, 3.5–5.5 cm wide, attached more firmly than the ultimate joints. Inner tepals 8–10, widely separated and not completely ringing the receptacle and not hiding the short outer tepals; inner tepals 2.5–3 × 1 cm, pale yellow-green, the margins essentially colorless and erose. Filaments bright green; anthers bright yellow, often stunted and lacking pollen. Flowering March and April. Fruits mostly 3–3.5 × 2–2.5 cm, yellow, solitary, leathery and moderately fleshy, strongly tuberculate, spineless or with slender bristle-like deciduous spines 9–15 mm long, becoming spineless or essentially so at maturity; fruits might persist for many months under favorable conditions, or soon falling away during drier conditions. Seeds variously present or absent.

Abundant and widespread on desert pavements, sandy plains and flats, bajadas, pediments, and rocky slopes of the hotter, drier mountains, and to at least 2725 feet in the Ajo Mountains and to 3150 feet in the Gila Mountains near the Tinajas Altas Mountains. It has been in the flora area for at least 15,700 years.

Southeastern California, southern Nevada, southern and western Arizona, eastern Baja California, northeastern Baja California Sur, and northwestern Sonora.

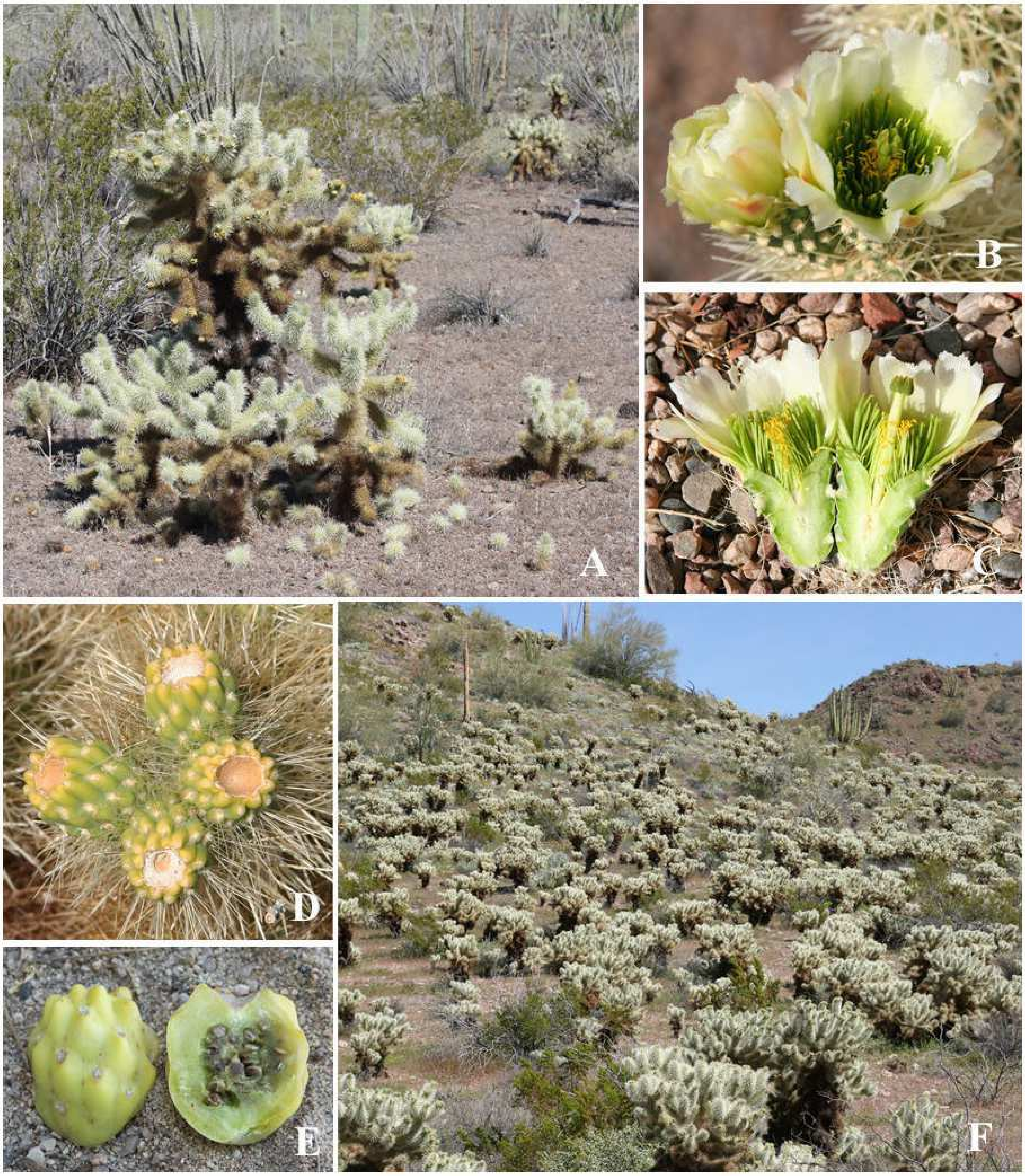

Figure 6. *Cylindropuntia bigelovii.* (A) Gunsight Hills, 15 Apr 2012. Organ Pipe headquarters: (B & C) 18 May 2006; (D & E) 23 May 2010. (F) Bates Well Road, W of Bates Well, 20 Mar 2005.

This cholla is primarily a clonal species. The upper or younger joints fall at a touch, and the spines are difficult and painful to pull out of your flesh. The plants propagate prolifically from readily-rooting fallen joints. The resulting mine-field of spines is a serious hazard to the walker. This most feared plant of the flora area is nonetheless lovely when the dense cover of spines catch the early- or late-day sun, creating a golden halo. Yet you need only one encounter with this fierce cholla to forever change your behavior: never again will you take a step back without first looking behind you. In southern Arizona this cactus is often called jumping cholla. Here's why: you could easily pick up a joint of *C. bigelovii* on, say, your *left* boot while walking, un-noticed until your natural gait deposited the joint onto the back of your *right* leg (calf or pants, depending), about a foot off the ground. Hence the name jumping cholla–how else did it get up there? Hornaday (1908: 221) called it, "Bigelow's Accursed Cholla" and said, "The worst thing about that Cholla is its treachery." Half a century earlier, Bigelow (1856: 13) himself wrote, "We find (February 7) a new species of *Opuntia* (described by Engelmann as *O. bigelovii*), with a reticulated woody stem, very fragile at the joints before hardening into wood, and armed with spines worse than those of a porcupine. It is called by the Mexicans, 'chug.' The plant is the horror of man and beast. Our mules are as fearful of it as ourselves. The barbed spines stick so fast in the flesh that the joint of the plant is separated from the main stem before the spines can be withdrawn." They were somewhere between the area of Wikieup (Mohave County, Arizona) and what is now the Alamo Lake area (La Paz County).

All plants sampled at Organ Pipe Monument (by Marc Baker) are triploid (Pinkava et al. 1992a); consequently there is very little chance of the seeds being viable. Pollen production is highly variable in this species; at least the triploid plants produce relatively few pollen grains. In the Tucson region pollen production may be higher in seasons of high rainfall and lower during drier periods (Mary Kay O'Rourke, in Felger & Zimmerman 2000). In addition, populations of *C. bigelovii* within the Tucson area appear to be primarily diploid (Baker et al. 2009). It has been suggested that the success of triploid apogamy, which is a common occurrence in *C. bigelovii*, *C. fulgida*, and *C. leptocaulis*, lies in its ability to fix and maintain particularly adaptive genomes (Baker & Pinkava 1987). *Cylindropuntia bigelovii* and *C. fulgida* have fewer inner tepals than most other chollas. Reduction in the perianth correlates with asexual reproduction, as might be expected with reduced selection pressure by pollinators. *Cylindropuntia bigelovii* has thicker, generally shorter, and more densely spiny joints and extends into more arid regions than does *C. fulgida*.

The Cahuillas pit-baked the buds (Bean & Saubel 1972) and Seris pit-baked young stem segments and made a diuretic tea from the roots (Felger & Moser 1985). O'odham and Seri graves were often covered with brush and chollas, often this species, to discourage animals such as coyotes from digging (Felger & Moser 1985; Rea 1997). Gila River Pimas used pieces of this cholla as barricades against marauding animals in their fields (Rea 1997).

OP: 1.8 km NW of Red Tank Well, 5 Mar 1988, *Baker 7582* (ASU, ORPI). 2 km NW of Dripping Springs, 7 Mar 1988, *Baker 7588* (ASU, ORPI). W slopes of Diablo Mts, 2 Dec 1990, *Felger* (observation). †Puerto Blanco Mts, on ridge, seeds, 980 to 10,500 ybp (7 samples).

CP: Agua Dulce Mts, 1200 ft, 14 Apr 1941, *Benson 10766.* Cholla Pass, 3.8 km ESE of Sheep Mtn, 325 m, 5 Jul 2000, *Baker 13839* (ASU, SD). Cholla Pass, 11 Apr 1978, *Lehto L22500* (ASU). Observations, *Felger*: Eagle Tank, 13 Jun 1992; Childs Mt, 2845 ft, 18 Aug 1992.

TA: Tinajas Altas, 14 Feb 1894, *Mearns 348* (US). 0.5 km N of Tinajas Altas, 12 Feb 1977, *Reeves 5393* (ASU). Flats at SW side of Tinajas Altas range, 10 Jan 2002, *Felger* (observation). †Tinajas Altas, seeds, 1230 to 15,680 ybp (10 samples). †Butler Mts, spines, seeds, 11,060 ybp.

Cylindropuntia echinocarpa (Engelmann & J.M. Bigelow) F.M. Knuth
[*Opuntia echinocarpa* Engelmann & J.M. Bigelow. *O. wigginsii* L.D. Benson]
Silver cholla. Figure 7.

Small chollas, often 20–75 (100) cm tall, and usually shorter in the driest, western areas where the plants are often dwarfed. Primary stem(s) of larger plants mostly erect, or sometimes stiffly horizontal just above the soil surface. Joints (1.5) 5–13 × 1.8–3.2 cm, firmly attached or smaller ones sometimes readily detaching; stem tubercles 12–16 mm long, usually less than twice as long as broad. All areoles densely spiny; spines whitish to yellow and densely covering and obscuring the stem segments; spine sheaths yellowish or whitish (silvery). Flowers 1–4 from a single joint; often 5.5–6.5 cm wide. Inner tepals about 2 cm long, shiny pale greenish yellow to silvery white. Filaments green to greenish yellow (not brilliant green as in *C. bigelovii*); anthers yellow. Flowering March and April. Fruits often 15–20 × 17–22 mm, dry upon ripening in late May and early June, bur-like with bristly spines, and not persistent. $2n = 22$.

Widespread and common across the Tinajas Altas region and the western part of Cabeza Prieta; sandy flats, dunes, creosotebush flats, hills, and mountain slopes. This cholla does not range eastward from Cabeza Prieta in the flora area, but does occur to the northeast in Maricopa County.

Western Arizona, northwestern Sonora, northeastern Baja California, southeastern California, southern Nevada, and southwestern Utah.

The flower buds and young cladodes were prepared in a similar manner as those of *C. acanthocarpa* and often constituted a staple food in spring (Castetter & Bell 1942; Castetter & Underhill 1935).

This species commonly hybridizes with *C. acanthocarpa*, as discussed under that species, to a much lesser extent with *C. leptocaulis* (e.g., *C. echinocarpa* × *C. leptocaulis*, Lechuguilla Desert north of Wellton Hills, Yuma Co., 10 Jan 1994, *Baker 11275* (ASU), and very rarely with *C. ramosissima* (the first documented specimen of *C. echinocarpa* × *C. ramosissima* is from Clark Co., NV, 20 Apr 2012, *Baker 18102*, specimen to be deposited at ASU).

CP: T13S, R14W, S24, 6 Apr 1979, *Lehto L23485* (ASU). 0.8 mi SE of Tule Well on Camino del Diablo, 16 Jun 1992, *Felger 92-623*. 24.5 mi SW of boundary with Organ Pipe en route to Pinta Sands, 4 Mar 1995, *Rebman 2881* (ASU, DES, SD). Observations, *Felger*: Christmas Pass, 14 Jun 1992; Pinta Sands, 1 Feb 1992.

TA: SE side of Tinajas Altas Mts, 32°18'N, 114°02'W, 3 Feb 1990, *Felger* (observation).

Cylindropuntia fulgida (Engelmann) F.M. Knuth
[*Opuntia fulgida* Engelmann]
Chain-fruit cholla, jumping cholla; *choya*; hanamĭ

In southern Arizona this cactus is generally called chain-fruit cholla, and the name jumping cholla generally is reserved for *C. bigelovii*.

This species ranges from southern Arizona to northwestern Sinaloa. (The single specimen from southwestern New Mexico [*Bird 3341*, UNM] is of questionable provenience and identification, or possibly adventive [Allred & Ivey 2012].) Variety *fulgida* apparently does not extend south of the Guaymas region in Sonora. Seeds resembling *C. fulgida* (little wedges crammed together) have been found in the Puerto Blanco Mountains dating to 3400 years old. Although in most cases the varieties are readily distinguished, *C. fulgida* var. *mamillata* probably does not deserve taxonomic recognition, as it is merely a form interspersed among the typical forms, except that the *mamillata* form becomes dominant toward the southern part of the geographic range of the species. *Cylindropuntia fulgida* is replaced in the Baja California Peninsula by the closely related and similar-appearing *C. cholla* (F.A.C. Weber) F.M. Knuth.

OP: †*C.* cf. *fulgida*, Puerto Blanco Mts, on ridge, seeds, modern (30) to 3400 ybp (6 samples).

Figure 7. *Cylindropuntia echinocarpa*. (A & C) Dunes 20 mi S of Sonoyta on Hwy 8, Sonora, 27 Mar 2010. (B) W side of Gila Mts, 16 Mar 2013, photo by Jim Malusa.

1. Spines dense, interlaced, and obscuring the stem surface, with loose-fitting papery sheaths, the larger spines usually 2.5–3.5 cm long…….................................. **Cylindropuntia fulgida** var. **fulgida**
1. Spines relatively sparse, not interlaced, and not obscuring the stem surface, with tight-fitting (not papery) sheaths, the larger spines 1–2 cm long…................... **Cylindropuntia fulgida** var. **mamillata**

Cylindropuntia fulgida var. **fulgida**
[*Opuntia fulgida* var. *fulgida*]. Figure 8.

Shrubby to arborescent chollas, often 1–2.5 (rarely to 4+) m tall; trunk well developed, reaching 25 cm diameter, and often with several major branches, and a broad, much-branched crown. (Some are tall enough that you can stand in the shade of a spreading cholla, being mindful of spiny joints overhead and fallen joints littering the ground.) Smaller branches and joints, mostly at the crown or top of the plants, the joints green all year, detaching at the slightest touch, earning the name "jumping cholla." The joints densely spiny, the spines usually obscuring the stem surface; spine sheaths large, golden yellow to straw colored; tubercles longer than wide and prominent; stem tissue often becoming blackish or gray on drying (nearly all herbarium specimens of *C. fulgida*, as well as the closely related *C. cholla*, are blackish or gray; also see *Carnegiea* and *Lophocereus*).

In Organ Pipe flowering primarily starts before the summer rains and continues into July, although flowering is documented in the region from late April through August. Flowers 2.5–5 cm wide. Inner tepals bright pink-purple, spreading widely and sometimes curling back, relatively few and not totally ringing the flower, the larger tepals often 14–20 × 6–7 mm. The tepals, stamens, and style usually fall as a unit. Filaments bright purplish pink, or the inner filaments sometimes white; anthers white. Stigma white. The flowers open in the late afternoon, sometimes not until 6 pm, remain open during the night, and wither before dawn, or they may also open in the early morning. Flowers visited by medium-sized moths at night and by medium-sized bees during daylight. Fruits green and fleshy, often 3–6 × 2–4.8 cm, mostly obovoid, remaining green and fleshy, usually persisting for at least several years and proliferating in hanging chains of (3) 6–18 fruits, the longer chains often swaying in the wind.

Widespread and often abundant, mostly in lowlands on bajadas, desert flats and along margins of large washes, and less common on rocky slopes and alkaline flats, and up to about 2775 feet in the Ajo Mountains; Organ Pipe and Cabeza Prieta westward to the vicinity of Tule Well. Bighorn sheep and Sonoran pronghorn relish the fruits and may depend on them for water (moisture) during extreme drought. This cholla is essentially at its western geographic range in Cabeza Prieta.

Propagation is vegetative from readily-rooting fallen joints and fruits (Toumey 1845). *Cylindropuntia fulgida* is mostly diploid, but triploid individuals are common. Diploid individuals of *C. fulgida* exhibit lower pollen fertility than do most other non-apomictic cholla species and triploid individuals exhibit even lower pollen fertility (Baker & Pinkava 1987). Although reproduction by seed has not been observed in the flora area it probably occurs to some extent. For a summary discussion of the life history of this species see Turner et al. (1995).

The fleshy fruits are available all year and were often a significant food resource for local people. The fruits were consumed fresh or cooked and could be dried and stored (Castetter & Bell 1942; Castetter & Underhill 1935; Felger & Moser 1985; Nabhan et al. 1982). Dried, black gum that accumulates on the stem from injuries is edible and has been much appreciated by Seris and Yaquis (Felger 2007; Felger & Moser 1985). This dried gum is ground, cleaned, and cooked, often in animal fat, or eaten uncooked with water added. The stems, gum, fruits, and roots also have been used medicinally (Felger 2007; Felger & Moser 1985).

OP: Bates Well, 20 Nov 1939, *Harbison 26170*. 13 mi S of Rocky Point Junction [Why], 19 Aug 1961, *Tschirley T-80*. Vicinity of Aguajita, 29 Mar 1988, *Felger 88-130*. Estes Canyon picnic area, 16 May 1989, *Baker 7753* (ASU). Observations, *Felger*: Hwy 85 at N boundary of Monument, 23 May 1991; Hocker Well, 3 m tall, chains of 9–18 fruits, 3 Dec 1990.

CP: 7 mi E of Papago Well, 14 Mar 1937, *Harbison 17059* (SD). Cholla Pass, 11 Apr 1978, *Lehto L-22499* (ASU). 5 mi E of intersection at Tule Well along Camino del Diablo, 5 Mar 1995, *Rebman 2888* (ASU, DES). Observations, *Felger*: Bajada and on N side of Agua Dulce Mts, 31 Jan 1992; 6 mi eastward from Tule Well on Camino del Diablo, 28 Nov 2001.

Figure 8. *Cylindropuntia fulgida* var. *fulgida*. (A & B) Hwy 85 at mile marker 68 [10 highway mi S of N boundary of OP], 7 Jun 2006. (C) Chain of fruits, trail to Victoria Mine, Puerto Blanco Mts, 28 Feb 2009. (D) Between Hwy 85 and Armenta Ranch, 30 Jul 2013. (E) Coffeepot Well, BLM land, 28 Apr 2006.

Cylindropuntia fulgida var. **mamillata** (Schott ex Engelmann) Backeberg
[*Opuntia fulgida* Engelmann var. *mamillata* (Schott ex Engelmann) J.M. Coulter]. Figure 9.

Rare in the northeastern part of Organ Pipe where it occurs as single plants or groups of less than about 10 plants. In this region plants of var. *mamillata* are shorter than those of var. *fulgida*. Variety *mamillata* is more common immediately eastward and northward from the Monument border. A nearby population extends for several miles west of Quijotoa near Arizona Hwy 86 and there is a very large population near Coffee Pot Mountain in the Sauceda Mountains in the Goldwater Range.

OP: Near Kuakatch, 2 m tall, 10 Apr 2000, *Rutman* (photo). Hwy 85 near milepost 67 (near N boundary), one plant, 27 May 2001, *Rutman* (photo).

Figure 9. *Cylindropuntia fulgida* var. *mamillata*. Near Coffeepot Mtn, 28 Apr 2006.

Cylindropuntia leptocaulis (de Candolle) F.M. Knuth
[*Opuntia leptocaulis* de Candolle]
Desert Christmas cholla; *tasajillo*; 'ajĭ vipinoi, ce'ecem vipinoi. Figure 10.

Slender-stem chollas, 0.5–1 m (reaching 1.5+ m when growing through shrubs). Young plants with a single, somewhat tuberous root. Mature plants somewhat shrubby or often strict, with main branches long, straight, erect to sub-erect, and arising from near plant base. Young stems (joints) 4.8–6.6 mm diameter (sometimes shriveling to 3 mm in drought), green all year, the surfaces relatively smooth with low, poorly defined tubercles. Areoles spineless or producing a single spine often 1.5–8 cm long with a deciduous yellowish sheath. Larger and longer branches often bearing many and much smaller "short shoots" (joints), these mostly at right angles to the main axes, readily detaching, and often bearing glochids but no spines.

Flowers 1.5–2 cm wide, usually opening late in the afternoon or near dusk and remaining open in the early evening (in late May observed opening at 4 p.m. and closing at 7:30 p.m.). Inner tepals about 1 cm long, pale yellow-green to cream-white; outer tepals red-purple. Stamens very sensitive, rapidly converging when touched. Filaments, anthers, style, and stigma cream colored. Flowering April and May and after summer rains. Fruits mostly ripening November and December, and often persisting at least until May, or some fruits retained all year. Fruits (10) 14–22 × 8 mm, broadly ellipsoid to obovoid, fleshy, the skin red, the pulp pale yellow-orange, with widely separated areoles bearing tufts of small glochids; often also with larger fruits 25–30 × 8.5–10.5 mm, obovoid to clavate; both classes of fruits several-seeded or sometimes seedless, and sometimes producing a short green joint or a second fruit from 1 or more of the upper areoles. Seeds 4.3–4.5 mm diameter. The small, fleshy fruits, red when ripe, can be eaten fresh, after removing the glochids (Chico Suni in Felger et al. 1992; Rea 1997).

This species is notable for its slender stems and small, fleshy, red fruits often on "short shoots" along the length of the longer, terminal stems. It is not very formidable in appearance, but when tucked into a runnel among creosotebush and bursage, it is painfully easy to blunder into a spiny Christmas cholla.

Figure 10. *Cylindropuntia leptocaulis.* (A, C, & E) Bajada W of Sikort Chuapo Mts, 4 Mar 2009. Hwy 85 near N boundary of Organ Pipe: (B & D) 22 May 2006; (F) 21 Mar 2010.

Widespread in many habitats in Organ Pipe and Cabeza Prieta including sandy to gravelly, silty or rocky soils of washes, canyons, bajadas, creosotebush flats, and slopes; often growing in association of shrubs and desert trees. The series of years prior to about 2010 with below-average rainfall caused a widespread die-off of this cactus throughout the flora area. It was in the Puerto Blanco Mountains about 1000 years ago. There are two chromosome races in the flora area, diploid and triploid, which are morphologically indistinguishable and occur intermixed (Baker et al. 2009).

Arizona to Oklahoma and Texas, and Mexico southward to northwestern Sinaloa and Puebla. This is the most slender-stemmed of the chollas and the most wide-ranging geographically. Despite geographical and cytological variation, it does not seem practical to recognize infraspecific taxa, although Bravo-Hollis (1978) lists eight varieties. Reports of *Cylindropuntia leptocaulis* from the Baja California Peninsula refer instead to the closely related *C. lindsayi* (Rebman) Rebman. Although this species hybridizes with several others, only hybrids with *C. echinocarpa* have been recorded from vicinity of the flora area (see *C. echinocarpa*).

OP: Cipriano Well, *Nichol 27 Apr 1939* (ORPI). ¼ mi N of Kuakatch Wash Road on power line road, 24 Jul 1978, *Bowers 1383* (ORPI). 0.9 mi W of Quitobaquito, 14 Sep 1988, *Felger 88-470*. Observations, *Felger*: Dos Lomitas, 23 May 1991; Hocker Well, very common, 3 Dec 1990. †Puerto Blanco Mts, on ridge, stems, 30 & 990 ybp (it presently grows in the nearby canyon bottom and not on the slopes or ridge).

CP: Tule Wells, 11 Mar 1937, *Harbison 16832* (SD). Observations, *Felger*: Agua Dulce Mts, 31 Jan 1992; Namer's Grave, 1 Feb 1992; 3 km WNW of Little Tule Well, Packrat Hill, near Dos Playas, and Mohawk Valley, 12 & 13 Jun 1992. 3.1 mi W of the intersection at Tule Well along the Camino del Diablo, 5 Mar 1995, *Rebman 2886* (ASU, DES, SD).

††**Cylindropuntia multigeniculata** (Clokey) Backeberg

This low shrub cholla grew in the Ajo and Puerto Blanco Mountains at least 9600 to 32,000 years ago in *Yucca brevifolia–Juniperus californica* woodland that may have been similar to the present day habitat for *Cylindropuntia multigeniculata,* which occurs in Mohave County, Arizona, and Clark County, Nevada. The fossil material was originally thought to be of *C. whipplei* (Engelmann & J.M. Bigelow) F.M. Knuth (Felger et al. 2013b; Van Devender 1987, 1990), but was identified as *C. multigeniculata* by Marc Baker in 2013. See Baker and Cloud-Hughes (2014) for identification and description of *C. multigeniculata* and relationships with other spiny-fruited chollas.

OP: †Alamo Canyon, seeds, 9570 to 32,000 ybp (4 samples). Montezuma's Head, 13,500 to 21,840 ybp (4 samples.) †Puerto Blanco Mts, on ridge, stems, seeds, 14,120 ybp.

Cylindropuntia ramosissima (Engelmann) F.M. Knuth
[*Opuntia ramosissima* Engelmann]
Diamond cholla. Figure 11.

In California this cactus is often called pencil cholla (Pinkava 2003a), a name reserved for *C. arbuscula* in Arizona. Slender-stem chollas often 0.3–0.8 (1.2) m tall, usually broader than tall, sometimes with short, thick, woody trunks, the principal branches mostly basal; sometimes forming spreading colonies. (Individuals of this species, if left unmolested, generally form a single-trunked shrub but the substrate underneath the plants are often a preferred site for the nesting of rodents. The rodent activities can cause the plant to topple and produce new roots where its younger stems touch the soil.) Stem segments (joints) firmly attached, 6.5–9 mm diameter, dull greenish to gray-green. Spines on some joints sometimes none, or 1 per areole in upper portion of each joint, (1.5) 2–8.5 cm long, with deciduous straw-colored sheaths. Areoles linear, recessed, each forming a conspicuous longitudinal groove in the upper end of its subtending tubercle, the glochids mostly buried in the groove; young stem and floral areoles with small, dense tufts of white hairs. Tubercles very low but sharply defined, their outlines diamond-shaped (hence the common name).

Figure 11. *Cylindropuntia ramosissima.* (A) S of San Cristobal Wash, N of Camino del Diablo, 27 Dec 2013. (B) Crater Range, near Hwy 85, 31 Jan 2009. Collected 18 km NNE of Amboy, San Bernardino Co., CA and relocated to Prescott, AZ, *Baker 17047.1*: (C) 27 Jul 2010; (E) near ripe fruits, 7 Sep 2010; photos by Marc Baker. (D) Anza Borrego Desert State Park, photo by Bill Sullivan for ABD Natural History Assoc.; (F) East of San Cristobal Wash and north of Camino del Diablo, 23 Nov 2013.

Flowers 2.5–3 cm wide. Inner tepals pale yellow-brown to cream-color, some suffused medially near apex with red-purple. Filaments bright green, the anthers bright yellow. Style and stigma cream colored. Flowering late April and early May and often after summer rains; flowers opening in mid- to late afternoon, often about 3 p.m. and closing 1–2 hours after sunset. Developing fruits with accrescent spines; mature fruits characteristically dry, 17.5–42 × (6.5) 8.3–10.7 mm, mostly persistent, densely spiny, the longer spines 14–22 mm. Fruits ripening late May and June or after summer rains. During the exceptionally wet El Niño year of 1991–1992, ripe, fleshy fruits persisted until late January and early February.

Common in scattered localities across the lowlands of Cabeza Prieta and Tinajas Altas, mostly on well-drained soils of valley plains, flats, and bajadas, and sometimes on low hills. Especially common along the western side of the Lechuguilla Valley in the Goldwater Range and the Tinajas Altas region. Also two records at the western margin of Organ Pipe where it grows in sandy soil. Both diploid and tetraploid races of *C. ramosissima* occur in the flora area. No morphological characteristics have been found to distinguish the two races, although tetraploid individuals tend to occur on sandy substrates and diploid individuals tend to occur on rocky substrates (Baker et al. 2009). Diamond cholla at the latitude of the flora area halts its eastern march along the western reaches of Organ Pipe, although it does range farther eastward in central Arizona. It has been in the Tinajas Altas region for more than 10,000 years.

There was also widespread and significant die-off of *Cylindropuntia ramosissima* from the north end of the Growler Mountains through the San Cristobal Valley, with greater than 90% mortality in the valley, but less towards the Growler Mountains. In March 2014, Rutman found a clonal colony about 10 m wide, due to root crown spreading, near the northern tip of the Growler Mountains in the Goldwater Range. It was located on a lower bajada with a Pleistocene surface with *Ambrosia deltoidea*, *A. dumosa*, *Krameria bicolor*, and *Larrea*.

Western Arizona, southeastern California, southern Nevada, southwestern Utah, northwestern Sonora, and Baja California.

Bean and Saubel (1972) report that the fruits were eaten fresh or dried for later use. The stems, with the spines removed, were boiled into a soup or dried for future use. However, the fruits very quickly become dry on maturing and hardly seem edible when fresh—there obviously is a lot we don't know about the intricate relationships of people and plants in our deserts.

OP: W of Bates Mts, sandy flat, 23 Mar 1990, *Baker 7776* (ASU, ORPI).

CP: 7 mi E of Papago Well, *Harbison 15 Nov 1937* (SD). Lower Well, *Simmons 17 May 1963* (CAB). San Cristobal Wash on road to Papago Well, 31 Jan 1992, *Felger 92-3*. 2 mi on Charlie Bell Road WNW of Little Tule Well, 12 Jun 1992, *Felger 92-539*. Cabeza Prieta Mts, 14 Jun 1992, *Felger* (observation). Growler Valley, 1.4 mi W of W boundary of OP on Camino del Diablo/Bates Well Road, *Rutman 28 Sep 2013*.

TA: E end of Tinajas Altas Pass, 12 Feb 1977, *Reeves 5394* (ASU). SW side of Tinajas Altas range, flats adjacent to granitic hills, 10 Jan 2002, *Felger* (observation). Camino del Diablo SE of Raven Butte, 25 Oct 2004, *Felger 04-08*. †Butler Mts, stem, 10,360 ybp.

Cylindropuntia spinosior (Engelmann) F.M. Knuth
[*Opuntia spinosior* (Engelmann) Toumey]
Cane cholla. Figure 12.

Shrubby chollas to 1.8 m tall, the trunk erect or nearly so. Stems become purplish in winter and dry seasons. Joints 5–20 cm long and moderately thick, firmly attached, and often arranged in whorls. Flowers April and May, showy; inner tepals rose-purple, 1.8–3.5 cm long. Filaments rose-purple; anthers white. Fruits fleshy, yellow, knobby, spineless, and semi-persistent.

Widely scattered and rather rare on *Larrea* flats in Organ Pipe and the eastern margin of Cabeza Prieta in the vicinity of Adobe Well where it is locally common. It grows on clay loams on lower bajadas and upper valley floors, where this species is at its westernmost limit in southern

Arizona. However, it ranges farther west in northern Arizona. Perhaps the 1939 record from Quitobaquito is from a transplanted cholla because it has not been documented there since. Hybridization with *C. acanthocarpa* and *C. versicolor* is discussed under those species.

Figure 12. *Cylindropuntia spinosior*. (A) Why, 5 May 2005. Hwy 86 west of Quijotoa, Pima Co.: (B) 18 May 2006; (C & D) 1 May 2005; (F) 8 May 2006. (E) Hwy 85 near Why, 6 Nov 2013.

Widespread in Arizona, especially at and above the upper elevation limits of the desert. Also New Mexico, northern Sonora, and Chihuahua. The fleshy fruits are edible.

OP: Quitobaquito, 28 Nov 1939, *Harbison 26188* (ARIZ, SD). Growler Canyon, 19 Oct 1987, *Baker 7572* (ASU, ORPI).

CP: 0.8 km E of Adobe Well, 12 Jun 1992, *Felger 92-546* (ARIZ, AU).

Cylindropuntia versicolor (Engelmann ex J.M. Coulter) F.M. Knuth
[*Opuntia versicolor* Engelmann ex J.M. Coulter. *O. thurberi* Engelmann subsp. *versicolor* (Engelmann ex J.M. Coulter) Felger & Lowe]
Staghorn cholla; *siviri*. Figure 13.

Chollas reaching 2–2.5 m tall with an open branching pattern; the stems become greenish purple in winter and dry seasons. Joints firmly attached, generally 5–15 cm long, the tubercles prominent. Inner tepals probably 2–2.5 cm long and variously colored (see below); filaments yellow-green, the anthers yellow. Flowering April and May. Fruits probably 2.5–4 cm long, fleshy, greenish, sometimes tinged with purple, persistent through most of the year, and often several clustered at a stem tip.

Figure 13. *Cylindropuntia versicolor*. Kitt Peak Road near Hwy 86: (A) 25 May 2010; (E & F) 28 Apr 2006. (B & C) Hwy 86 west of Quijotoa, 30 Apr 2005. (D) San Simon Valley, Hwy 86 E of San Simon, 6 Nov 2013.

A few, small, scattered populations are documented in Arizona Upland areas of Organ Pipe, where this cholla is at its westernmost limit and rare.

This cholla is common across much of southern Arizona but east of the flora area. South-central Arizona and Sonora southward to the Guaymas region. Flower buds and young stems were cooked and the fleshy fruits were eaten fresh (e.g., Castetter & Underhill 1935).

In southern Arizona the flowers can be yellow, yellow-green, or reddish, including the Tucson Mountains (the type locality) westward to the Kitt Peak Road area and elsewhere along Hwy 86, including the San Simon Valley. Farther south in Sonora the flowers are consistently yellow to yellow-green. Putative hybrids between *C. versicolor* and *C. acanthocarpa, C. leptocaulis*, and *C. spinosior* have been reported from outside the flora area (Grant & Grant 1971; Pinkava 2003a).

OP: Just W of Diablo Mts along Ajo Mt Drive, 650 m, 32°00'30"N, 112°44'W, 16 May 1989, *Baker 7752* (ASU). 0.2 m S of intersection of road to Cabeza Prieta Game Refuge on Bates Well Road, 3 Dec 1990, *Felger 90-579* (ARIZ, ASU).

Cylindropuntia cf. whipplei, see **Cylindropuntia multigeniculata**

Echinocactus

Barrel cacti, solitary or branched basally, with stout spines, diurnal flowers, and fruits mostly dry when ripe and conspicuously woolly. A genus of seven species in Mexico and southwestern USA; three species occur in Arizona including *E. horizonthalonius* Lemaire and *E. xeranthemoides* (J.M. Coulter) Engelmann (*E. polycephalus* var. *xeranthemoides* J.M. Coulter).

Echinocactus polycephalus Engelmann & J.M. Bigelow
Many-headed barrel cactus, cottontop cactus; *biznaga*. Figure 14.

Multiple-headed barrel cacti, 0.5–1 (2) m wide, the plants often with 6–50 (100+) stems or "heads." (A giant mound-shaped plant on a sandy plain near the western boundary of Cabeza Prieta measured 190 × 201 cm wide, 81 cm tall, and had more than 152 stems; Figure 14A.) Individual stems 9–12 (19) cm diameter. Spines nearly obscuring the stem surface, very stout, rigid, straight to slightly curved near the tip and often twisted but not hooked, ridged below to flattened, the central spine especially stout, often 5–8.5 cm long. Spine surfaces red but obscured by felt-like covering of overlapping, short, white hairs imparting a dull pinkish gray color. Young areoles densely white woolly, older areoles less so. Flowers about 5.5 cm long, confined between the dense spines and thus not opening fully, the inner tepals 2.4–2.6 cm long, the interior of the flower bright, clear yellow (inner tepals, stamens, stigma, and style), the outer tepals bristle-tipped and yellow with a reddish midstripe. Fruits densely and persistently white woolly, drying soon after maturity; fruits plus the persistent, aristate outer tepals 3.5–4 cm long. Seeds blackish (dark red-brown under magnification and bright light), (3) 3.5–4 mm maximum diameter, with a low ridge or crest, the seed surface papillate and often angled due to compression at time of development. Flowering late May and June.

Central and southwestern part of Cabeza Prieta and the Tinajas Altas region; sand flats and sandy soils of valley floors, rocky flats especially on desert pavements, bajadas, and sometimes in soil pockets among hills and lower slopes.

The short, white hairs on the spines suddenly become translucent when wet, revealing the blood-red spine surfaces (Figure 14C): the spines are red in the rain, but revert to their usual dull color when rain ceases. The flowers are confined by the dense spine cover and for this reason do not open as wide as most other cactus flowers. The dry, seed-bearing fruits are likewise tenaciously held among the closely set spines and may remain in place for one year or more. The seeds fall as the fruits disintegrate. The plants generally flower profusely but in at least some years set few fruits. We

Figure 14. *Echinocactus polycephalus.* (A) Richard B. Laugharn and a plant with 152 stems, sandy plain in W margin of Cabeza Prieta, 28 Mar 2010, photo by Richard Felger. (B, E & F) Spine cluster and fruits, near Red Cone, Pinacate Biosphere Reserve, Sonora, 18 Jan 2009. (C) Wet spines, vicinity of Tinajas Altas, 22 Nov 2008, photo by Richard Felger. (D) Anza Borrego Desert State Park, San Diego Co., CA, photo by Bill Sullivan for ABD Natural History Assoc.

have not seen seedlings or small juvenile plants in the flora area, and presumably recruitment is a rare event.

Echinocactus, probably *E. polycephalus*, has been in the Tinajas Altas region for more than 43,000 years. Evidence from the fossils indicate these plants were more common on rocky slopes than today, which is more like the habitat of the Grand Canyon population, *E. xeranthemoides*, than that of *E. polycephalus*.

Echinocactus polycephalus is confined to some of the hottest, driest areas of the Sonoran and Mohave Deserts in northwestern Sonora, southwestern Arizona, southern Nevada, and southeastern California. It is replaced by *E. xeranthemoides* (J.M. Coulter) Engelmann (*E. polycephalus* var. *xeranthemoides* J.M. Coulter) to the north in Nevada and the Grand Canyon region in Arizona (Salywon & Hodgson 2012).

Some people in Yuma call it the "cannonball cactus." Large and small plants alike seldom re-establish after transplanting, and attempts to cultivate it in Tucson and Phoenix fail, probably due to too much rainfall. Sliced pieces of the stems were eaten, often boiled or pit-baked, by Hia C'ed O'odham and others. In "modern" times (probably during the first half of the twentieth century) the stems were made into cactus candy (Bean & Saubel 1972; Hodgson 2001; Zepeda 1985). The flower buds and seeds were eaten by the Cahuillas and others (Barrows 1900; Coville 1892).

Michele Lanan (pers. com. to Felger, 23 May 2014) verified extrafloral nectaries in *E. polycephalus* in late January 2014, in Inyo Co., California, at several sites along the Death Valley Road/Loretta Mine Road, from Big Pine along Hwy 190 to Death Valley. She observed numerous plants; some individuals had no nectaries, while others had a few per areole with ants near the stem apex. The presence of ants in January indicates some *E. polycephalus* EFNs might be active all year like those on *Ferocactus wislizeni.*

CP: 3.5 mi NE of Tule Well, low hills with desert pavement and very sparse vegetation, *Carnegiea gigantea, Fouquieria splendens, Larrea divaricata, & Olneya tesota*, 14 Jun 1992, *Felger 92-596.* 1.5 mi E of intersection at Tule Well along the Camino del Diablo, 5 Mar 1995, *Rebman 2887* (ASU, DES, UCR, SD).

TA: Tinajas Altas Mts, desert flats SW of mountains, Camino del Diablo (West Route), *Larrea tridentata, Ambrosia dumosa, Cercidium microphyllum, Fouquieria splendens, Olneya tesota, Opuntia ramosissima*, 12 Feb 1977, *Reeves 5426* (ASU). 0.5 km E of Camino del Diablo on road to Borrego Canyon, 4 Feb 1990, *Felger 90-20. Echinocactus* cf. *polycephalus*: †Butler Mts, seeds, 3820 to 11,060 ybp (5 samples). †Tinajas Altas, spines, seeds, 9700 to 15,680 (4 samples), & >43,000 ybp.

Echinocereus – Hedgehog cactus

Multiple-stem, spiny cacti, branching mostly from the base (those in the flora area). Spines several or more per areole, straight to curved, not hooked; areole glands absent. Receptacle spiny at anthesis, the spines not enlarging during fruit maturation. Flowers showy, medium-sized to large, adapted for daytime pollination, the stigma green. Fruits succulent and spiny, the dried perianth persistent; ripe fruits sweet and delicious, the spines falling away when the fruit ripens. Seeds blackish, tuberculate, rounded to obovoid.

The genus ranges from tropical to temperate regions in Mexico and western United States. The taxonomy is complicated due to fuzzy taxonomic boundaries, polytypic taxa, and differing interpretations by specialists. Most North American botanists recognize about 50 species (e.g., Baker 2012a; Zimmerman & Parfitt 2003a), while the *Echinocereus* specialists in Germany recognize more than 70 species (e.g., Blum et al. 1998).

1. Longer spines often 2.5–4 (5) cm, spines of a single color (straw-colored to gray); flowers red to red-orange; higher elevations in the Ajo Mountains. .... **Echinocereus coccineus**
1. Longer spines usually 4–10 cm, the central spine(s) similar or different in color from the radial spines; flowers pink or purplish; widespread.

    2. Spines dull yellow, brownish, and grayish, often bicolored, becoming (or remaining) gray (rarely blackish) with age; flowers usually deep magenta, very showy; seeds 1.3–1.5 mm long.. **Echinocereus engelmannii**
    2. Spines uniformly yellow, often blackish with age; flowers usually pale pink; seeds 1.1–1.3 mm long. .... **Echinocereus nicholii**

Echinocereus coccineus Engelmann subsp. **santaritensis** (W. Blum & Rutow) M.A. Baker, **comb. et stat. nov.** *Echinocereus santaritensis* W. Blum & Rutow, in W. Blum, M. Lange, W. Rischer, & J. Rutow, Echinocereus Monographie [Fa. Proost, Turnhout, Belgium], 373–375, 1998. Herbarium for the holotype corrected from UA to ASU in Der Echinocereenfreund 12: 93, 1999.

Santa Rita claret-cup cactus. Figure 15.

Multiple-stem hedgehog cactus usually branching from the base. Stems generally less than 30 cm long and average 5.5 cm wide, generally with 9 or 10 ribs, rather densely spiny, with the areoles on the same rib about 1 cm apart. Spines straw-colored to gray, each spine of one color, generally 3 or 4 centrals and about 10 radials per areole, longest centrals 2.5–4 (5) cm (generally ca. 3 cm long) and 0.6 mm thick. Flowers moderately bilaterally symmetrical (moderately zygomorphic), 5–11 cm long, 3–4 cm wide, bisexual, with a long style averaging 5 cm long, the inner tepals bright red to orange-red, flowering in April. Tetraploid, $2n = 44$ (Baker 2006).

Ajo Mountains above 1070 m on bedrock cliffs, cliff ledges, rocky slopes, and boulder outcrops, often growing near *Juniperus arizonicus* and *Vauquelinia californica*. This is the westernmost locality for subsp. *santaritensis*.

Subspecies *santaritensis* is widespread in mountains eastward in southern Arizona including the Atacosa, Chiricahua, Huachuca, Pajarito, Patagonia, Pinal, Pinaleño, Santa Catalina, Santa Rita (type locality), and Tucson Mountains, and in adjacent north central and northeastern Sonora.

The *Echinocereus coccineus* complex includes about one half dozen red-flowered, tetraploid and hexaploid species or infraspecific taxa. These are mostly montane cacti in Arizona, Colorado, New Mexico, Texas, and Utah, and southward in the Sierra Madre Occidental to Jalisco, and in northern Baja California. The differences between *E. santaritensis* and *E. coccineus* subsp. *coccineus* intergrade over an extensive geographical range in central Arizona, which suggests that *E. santaritensis* is better placed as a subspecies of *E. coccineus*. Most populations of *E. coccineus* subsp. *coccineus* have at least some individuals with pollen-sterile flowers, while those of *E. coccineus* subsp. *santaritensis* have only individuals with bisexual flowers. Flowers of *E. coccineus* subsp. *santaritensis* have mostly long styles (5 cm) and the areoles of the pericarp possess hairs that are longer than the subtending scale leaf, while those of subsp. *coccineus* have styles less than 4 cm long and the areoles of the pericarp have hairs that are shorter than the subtending scale leaf.

Echinocereus santaritensis has been listed as synonym of *E. polyacanthus* Engelmann by Anderson (2001). According to Sánchez et al. (2013), populations of *E. polyacanthus* are restricted to north-central Mexico. Although the areoles of the pericarpel in both species have long hairs that exceed the subtending leaf, flowers of *E. polyacanthus* are short and polymorphic (some individuals with pollen-sterile flowers and some with pollen-fertile flowers), while the flowers of *E. santaritensis* are long, pollen fertile and probably always perfect.

OP: 1.7 km S of Mt Ajo, 3600 ft, NW-facing cliffs of pink-brown rhyolite, associated species: *Achnatherum speciosum, Acourtia wrightii, Agave deserti, Aloysia wrightii, Artemisia ludoviciana, Crossosoma bigelovii, Cylindropuntia acanthocarpa, Echinocereus nicholii, Eriogonum wrightii, Ferocactus emoryi, Fouquieria, Gnaphalium canescens, Juniperus coahuilensis, Mammillaria grahamii, Notholaena standleyi, Opuntia chlorotica, Pellaea truncata, Rhamnus crocea, Simmondsia chinensis, Vauquelinia californica, and Viguiera parishii;* locally approx. 10 individuals, generally on inaccessible shelves and cliff faces, 27 Apr 2001, *Baker 14050* (ASU). N-facing slope above Bull Pasture, 10 Apr 2005, *Rutman 2005-0410-21* (ORPI).

AZ: **Santa Cruz** Co.: "*Echinocereus coccineus* Engelm., *sensu lato* (including *E. polyacanthus* Engelm.), det. Allan D. Zimmerman, February 1997. Plant and unattached flowers presented to Zimmerman in 1996 with the following field data: . . . Santa Rita Mountains: Coronado National Forest, Madera Canyon . . . . ca. 1650—1700 m . . . mostly in bud, flowers widely open at 10:30 a.m., 16 April 1996 (at beginning of blooming season), Jürgen Rutow & Michael Lange view this collection as the prospective **type** for a taxonomic split (preserved by ADZ in 1996; VOUCHER for a horticultural cutting in ADZ's living research collection), *Jürgen Rutow 52/96*" (holotype of *E. santaritensis*, ASU 211396; note that the protologue incorrectly indicates the holotype is at "UA," which was later corrected to ASU).

Figure 15. *Echinocereus coccineus* subsp. *santaritensis*. Ajo Mts above Bull Pasture, 10 Apr 2005.

Echinocereus engelmannii (Parry ex Engelmann) Lemaire subsp. **engelmannii**
[*E. engelmannii* var. *acicularis* L.D. Benson. *E. engelmannii* var. *chrysocentrus* (Engelmann & J.M. Bigelow) Rümpler]
Strawberry hedgehog cactus; *pitayita*; 'isvigĭ. Figure 16.

Several to many stems branching mostly from near the base, the stems 15–45 cm tall, about 7 cm wide, with a moderate to dense spine cover. Spines dull yellow to brownish, whitish, or grayish, becoming (or remaining) grayish with age, each areole generally bearing spines of various colors. Central spines (2)3–6(9), the longer (lower), central spine 3–10.5 cm long, often becoming whitish

Figure 16. *Echinocereus engelmannii*. (A & D) S of Scarface Mtn, Organ Pipe, 11 Sep 2013. N end of Little Ajo Mts: (B) 27 Mar 2005; (E) dried fruit, 17 Jul 2013. (C) Fresh fruits, Kuakatch Wash near Hwy 85, 23 May 2012.

with age, twisted or straight, flattened or terete, the other spines terete. Flowers showy, 7.5–9 cm long, 5–9 cm wide; inner tepals 4–7.5 × 1.5–2 cm, generally bright purple-magenta (sometimes varying from pink to darker colored in the same population). Fruits at first spiny, the spine clusters falling away at maturity, the pulp infused with pink or red from the red fruit skin. Seeds 1.3–1.5 mm long. Flowering March and early April; fruits ripe late May and early June. Upon ripening the fruit pulp and seeds are promptly consumed by a variety of animals, especially birds that poke a hole in the side of the fruit. Ants quickly finish off what the birds leave, and hollowed-out fruits are common.

Widespread and common across the entire flora area in many habitats, from lowest to high elevations. Usually on rocky substrates but also in deep, sandy-silty soils; mountains, hills, bajadas, desert flats, and sometimes upper floodplains of larger washes. Often growing with *E. nicholii* in the Puerto Blanco Mountains and elsewhere.

Western Arizona, southern California, Nevada, southwestern Utah, Baja California, northeastern Baja California Sur, and northwestern Sonora.

The fruits are delicious and are edible fresh together with the small seeds (Felger & Moser 1985; Rea 1997). The cooked stems were also eaten. "They ate the meat of the hedgehog cactus . . . like potatoes. . . . Shave them and then you cut them . . . and put salt on them" (Betty Melvin in Zepeda 1985: 61). Considerable quantities of seeds were found at a Hohokam site near Phoenix, suggesting cultivation and use as a trade item (Gasser 1982; Gasser & Kwiatkowski 1991).

Varieties defined by Benson (1982) within *Echinocereus engelmannii* (sensu stricto) have little geographical or morphological foundation (Baker 2012a; Zimmerman & Parfitt 2003a). Individuals from lower elevations tend to have stouter spines and larger stems than those at higher elevations. At almost every type locality for names associated with *E. engelmannii* (sensu stricto), morphological variation encompasses two to several varietal descriptions. Populations of *E. engelmannii* subsp. *engelmannii* represent a western form with mostly three or more angled central spines. In central Arizona, it intergrades with populations of *E. engelmannii* subsp. *fasciculatus* (Engelmann ex S. Watson) W. Blum & Michael Lange, which represent an eastern form with one or two terete central spines. All chromosome determinations for *Echinocereus engelmannii* (sensu lato) throughout its range have been $2n = 44$ except for a small region, where it is $2n = 22$, from St. George, Utah to just across the border in Mohave Co., Arizona. No consistent morphological characteristics have been found that differentiate the two chromosome races.

OP: Quitobaquito and vicinity: 5 Mar 1940, *Peebles 14555*; 29 Mar 1988, *Felger 88-112*. Bates Well, 30 Mar 1978, *Bowers 1121*. Puerto Blanco Drive at old road to Dripping Springs, 12 Apr 1978, *Bowers 1256*. Puerto Blanco Mts, 2 km WNW of Dripping Springs, 1720 ft, $n = 22$ (meiotic count), 7 Mar 1988, *Baker 7584* (ASU, SD). N boundary of Monument, 0.2 km W of AZ Hwy 84, 2 Dec 1990, *Felger 90-502*.

CP: Childs Mt, 9 Apr 1993, *Felger 93-280*. Observations, *Felger*: Agua Dulce Pass, Heart Tank, Tuseral Tank, 12 & 14 Jun 1992; Sheep Mt, Sand over lava at E side Pinacate flow, 31 Jan 1992, Tule Tank, 2 Feb 1992.

TA: Tinajas Altas, 15 Apr 1932, *Blackwell 709*. Observations, *Felger*: Ridge above Tinajas Altas Canyon, 19 Mar 1998; Granitic bajada at SW side of Tinajas Altas Mts, 10 Jan 2002.

Echinocereus nicholii (L.D. Benson) B.D. Parfitt
[*E. engelmannii* (Parry ex Engelmann) Lemaire var. *nicholii* L.D. Benson]
Golden hedgehog cactus. Figure 17.

Larger plants with 16–24+ stems branching near ground level, forming clumps often reaching 0.50–1+ m wide. Individual stems 6–9 cm diameter, erect to ascending. Spines translucent-yellow, often golden, monochromatic, becoming blackish on older parts of the stem; central spines 4–6, the longer ones 4–7 cm long, often twisted and somewhat flattened. Flowers generally pink, smaller and much paler than those of *E. engelmannii* (sometimes varying from pink to magenta in the same population). Fruits ovoid, 2.3–3.4 × 1.7–2.3 cm, remaining spiny after ripening, the skin green, becoming somewhat bronze when fully ripe where exposed to sunlight, the pulp remaining whitish. Seeds 1.1–1.3 × 0.8–1.2 mm. Flowering March and April, the fruits ripening in June. $2n = 22$.

Mostly on steep rocky slopes and hills, often very common towards higher elevations, sometimes on pediments at the base of rocky hills, and especially on bedrock or other stable substrates with very little soil. Widespread in the mountains of Organ Pipe including the Ajo, Growler, Puerto Blanco, and Quitobaquito Mountains, and in the eastern part of Cabeza Prieta. The north side of Sheep Peak in the Growler Mountains in Cabeza Prieta supports an exceptionally dense and extensive population. It is not found on bajadas or valley bottoms. Often most numerous on north-facing slopes and growing with *E. engelmannii* as well as *Carnegiea gigantea*, *Cylindropuntia acanthocarpa*, *Ferocactus cylindraceus*, *F. emoryi*, *Mammillaria grahamii*, *Stenocereus thurberi*, and sometimes *Sclerocactus johnsonii*.

Southern Arizona eastward from our flora area to the Silverbell and Waterman Mountains west of Tucson and western Sonora southward to the Sierra Seri (opposite Isla Tiburón).

The fruits were eaten together with the seeds by Hia C'ed O'odham (Hodgson 2001), probably as a minor food resource. Hodgson (2001) found the fruits to be even sweeter and better-tasting than other hedgehog cactus fruits (Felger 2007).

Figure 17. *Echinocereus nicholii*. (A) Growler Canyon, Bates Mts, 9 Sep 2012. (B) Growler Mine, Bates Mts, 13 Sep 2013. (C) Middle Fork of Alamo Canyon, Ajo Mts, 26 Mar 2005.

Echinocereus nicholii is distinguished from *E. engelmannii* by its generally larger and more robust habit, monochromatic yellow spines that become blackish with age, smaller and pink flowers, and different seed morphology. (*Echinocereus nicholii* occasionally has flowers larger and darker than usual and somewhat resembling those of *E. engelmannii.*) Also, for all individuals tested within the flora area, those of *E. engelmannii* have been tetraploid and those of *E. nicholii* diploid.

OP: 1 mi E of Bates Well, 4 Mar 1940, *Benson 9901*. Alamo Canyon, 14 Mar 1941, *Benson 10672*. Bull Pasture Trail, 1 Apr 1978, *Bowers 1234*. 2.4 mi W of Hwy 85 on Puerto Blanco Drive, 19 Jun 1989, *Felger 89-220*. Quitobaquito Hills, 22 Feb 1990, *Felger 90-39*. Gunsight Hills, 2 Mar 2003, *Rutman 2003-206* (ORPI). Trail from The Cones to Mount Ajo, 4090 ft, 10 Apr 2005, *Felger* (observation).

CP: Childs Mt, 2240 ft, 9 Apr 1993, *Felger 93-280*. Observations, *Felger*: Sheep Peak, N side at higher elevations, not on S-facing slopes except at summit, 31 Jan 1992; Agua Dulce Pass, 12 Jun 1992.

†**Echinocereus** sp./spp.

All but one of the fossil samples are from the Middle to Late Wisconsin age in the Ajo and Puerto Blanco Mountains. They are perhaps members of the *E. coccineus* complex, or the youngest samples might be one of the other two present-day *Echinocereus* species.

OP: †Alamo Canyon, seeds, 1150 to 29,110 ybp (3 samples). Montezuma's Head, seeds, 13,500 & 21,840 ybp. Puerto Blanco Mts, on ridge, seeds, 2340 ybp.

TA: †Tinajas Altas, seeds, 1030 to 10,600 (5 samples), & >37,000 ybp.

Echinomastus, see **Sclerocactus**

Ferocactus – Barrel cactus; *biznaga*; jiavul

Three barrel cactus species occur in Arizona. These have a single stout stem (rarely 1 or few branches if the apical meristem is injured). Areoles at the stem apex have short hairs forming a felt-like indumentum and areoles near the top of the stem have smooth, conical, yellowish brown extrafloral nectaries tended by ants (e.g., Lanan & Bronstein 2013; Morris et al. 2005; Ness et al. 2006; Ruffner & Clark 1986). Flowers yellow, orange, or red. Fruits fleshy, ripening after a number of months; the dried perianth persistent on the fruits; fruit rind yellow-green when immature, yellow when ripe, the pulp (funiculi) white. Although the fruits do not dehisce spontaneously, a fruit removed from the plant is like a saltshaker, scattering seeds from a hole at the base (where the fruit was attached). Seeds blackish, smooth or pitted. Many animals feed on the fruits, including ground squirrels that often scamper up the spines to munch the fruits. $2n = 22$.

The genus includes about 25 species, southwestern United States from California to Utah and Texas and Mexico southward to Oaxaca.

People across the Sonoran Desert made use of these large cacti. The flower buds and flowers were cooked and sometimes dried and stored. The cooked buds and flowers have a flavor somewhat like that of Brussels sprouts. Sometimes the buds were eaten fresh, although they are bitter unless cooked. The seeds, rich in oil and protein, were ground into an oily paste. The fresh fruits are edible but very acidic or sour (Bean & Saubel 1972; Felger & Moser 1985). Barrel cactus stems were baked in a pit, and the "meat" sliced and eaten or the "pulp" otherwise cooked (Castetter & Underhill 1935; Rea 1997; Melvin in Zepeda 1985: 49). Palmer (1878) reported that Tohono O'odham boiled pieces of the pulp in saguaro or organ pipe fruit syrup. Emergency liquid can be extracted from *F. cylindraceus* and *F. wislizeni* stems, but according the Seris the juice from *F. emoryi* is highly toxic (Felger & Moser 1985; Hodgson 2001) and presumably stem tissue or liquid of that species would not be ingested, at least not uncooked.

"They would gather it, and cut the skin off, and cut up, slice up, the meat of the barrel cactus, and they would cook it, they would roast it inside a pit sometimes, and then more recently they made candy out of it, the cactus candy" (Betty Melvin in Zepeda 1985: 49, 58). "You can cut the meat of the barrel cactus and you can suck the water from it. . . . my cousin Willie told me. . . one time he and his friends were out hunting in the desert. . . and this animal [probably a desert bighorn] would ram into the cactus and break the skin of the cactus and busted the cactus down. They watched him and he started to lick and eat the meat of the cactus." For medicine, "that hivijuls, if you have a sore you take it. . . . When it is not hard yet, you put it on the sore. If the plant is hard, you boil it and then wash the sore with it. The sore will get better quickly" (Betty Melvin in Zepeda 1985: 80).

The barrel cactus species in our flora sometimes reach 1.5–1.7 m in height, but in more equable (less xeric) regions they sometimes reach 3 m in height (Lindsay 1955, 1996; Zimmerman & Parfitt 2003b). A methuselah fishhook barrel cactus (*F. wislizeni*) south of Tucson measured 11.5 ft (3.5 m) in height with a maximum diameter of 3.5 ft (1.07 m) (Pima Co., San Luis Mts, SSW of Arivaca, 3750 ft, *Peachey 15 Dec 1994*, ARIZ 315928).

1. Spines all robust and rigid, more or less uniform in thickness (none are bristly) .... **Ferocactus emoryi**
1. Spine clusters with slender, bristle-like spines in addition to the thick, rigid spines.

    2. Stem growing straight up; largest spines hooked or not, often markedly twisted; seed surfaces pitted, resulting in a conspicuous reticulate pattern; rocky substrates (hills and mountains).. **Ferocactus cylindraceus**
    2. Larger plants usually conspicuously leaning southward; largest spines in each areole usually hooked, seldom twisted; seed surfaces essentially smooth and only minutely reticulate; flats and open desert..**Ferocactus wislizeni**

Ferocactus cylindraceus (Engelmann) Orcutt
[*Echinocactus viridescens* var. *cylindraceus* Engelmann. *Ferocactus acanthodes* (Lemaire) Britton & Rose (an ambiguous name, Taylor 1979 and Zimmerman & Parfitt 2003). Not *Echinocactus acanthodes* Lemaire]
Desert barrel cactus. Figure 18.

Stem cylindrical, growing straight and erect, the larger plants taller than wide; flowering plants (20) 45–125 cm tall (sometimes to 150 cm in the hills above Quitobaquito), (20) 25–38 cm diameter. Young plants (to about 15 cm tall) often with 14 stem ribs, adult plants with 19–20 ribs. Central spines whitish, gray, pink, or dull red (bright red when wet) with yellow-white tips, or sometimes straw-yellow with broad red or pink bands. Central spines moderately curved, sometimes twisted, usually not strongly hooked (except on immature plants); longer central spines 4–8.5 cm. Areoles with 4 major thick, rigid central spines, these surrounded by smaller spines (subcentrals or large radials, depending on interpretation), these rigid and intergrading with the centrals; radials (outermost spines) mostly bristle-like. Flowers often about 4.5 cm long (smaller than those of the other two *Ferocactus* in the region); inner tepals pure yellow to more often yellow with a salmon to maroon midstripe, orange, or sometimes red and with a darker red midstripe. Filaments reddish or yellow. Anthers, style and stigma lobes yellow (including otherwise red flowers), pale red, or red-magenta. Seeds pitted. Usually flowering February–April, and less vigorously late summer–early fall.

Widespread and often common on rocky hills and mountain slopes, at all elevations in Cabeza Prieta, parts of the Tinajas Altas Mountains, and the drier mountains in Organ Pipe. Growing on various slope exposures but mostly on west- and south-facing slopes. Barrel cacti are scarce in the vicinity of the waterholes in the western part of the flora area, such as at Tinajas Altas and Surveyors

Tank in the Tinajas Altas Mountains and also at higher elevations above the waterholes. In these places most of the larger individuals occur on inaccessible cliffs and rock faces. Their scarcity near

Figure 18. *Ferocactus cylindraceus*. (A) Gunsight Hills near Hwy 85, 15 Apr 2012. Near Red Cone, Pinacate Biosphere Reserve; (B) 7 Mar 2009; (C) Garden in Ajo, 21 May 2006; (D) spines of a young plant, 10 May 2005 (*F. cylindraceus* is the only barrel species at Red Cone and elsewhere in the Sierra Pinacate, Felger 2000); (E) Granitic hill, W end of Javelina Mtn, Sand Tank Mts, Maricopa Co, 5 Mar 2005.

the tinajas is undoubtedly due to bighorn sheep, which dislodge the plants with their horns and eat the fleshy stem (e.g., Warrick & Krausman 1989). This barrel cactus has been in the flora area for more than 11,000 years. It was at least reasonably common in the Tinajas Altas region from about 11,000–3800 years ago, but its absence in younger middens indicates a decline in abundance and it is still locally not common.

Populations in the flora area and nearby northwestern Sonora show the following patterns: Those in volcanic regions, on darker lava rock are characterized by elongated, twisted, stout, and reddish to pink or gray spines; some have bright yellow inner tepals, most are orange or yellow with a red midstripe, and some have bright red-orange to red inner and outer tepals. Plants on granitic hills and mountains generally have dull-colored, mostly straw yellow, and relatively shorter and more slender spines, consistently yellow inner tepals, and yellow or somewhat reddish filaments.

Southeastern California, southern Nevada, southwestern Utah, western Arizona, Baja California, and northwestern Sonora.

Across most of its geographic range this species characteristically occurs on rock slopes, where the plants are firmly anchored in rock or rocky soils and the plants grow straight up and not leaning like those of *F. wislizeni*. There is considerable variation in spine size and shape, and spine and flower color, but the colors and other features are apparently consistent within a local population and correlated with rock type. Benson (1982) recognized three varieties in the USA and one in Baja California. Zimmerman and Parfitt (2003b: 246) stated, "The varieties recognized by L.D. Benson are not consistently distinguishable." Others disagree and recognize all or some of the varieties: cactus taxonomy is fluid and fun.

OP: Near Bates Well, 4 Mar 1940, *Benson 9895*. Quitobaquito Hills, 12 Sep 1988, *Felger 88-456*. †Puerto Blanco Mts, on ridge, seeds, 1910 to 9720 ybp (7 samples).

CP: 7 mi E of Papago Well, 15 Mar 1937, *Harbison 16848* (SD). Tule Tank, 1300 ft, 15 Apr 1941, *Benson 10809*. T13S, R14W, S24, 6 Apr 1969, *Lehto L23489* (ASU). Observations, *Felger*: Agua Dulce Pass, Buckhorn Tank, Cabeza Prieta Tanks, Eagle Tank, 13–15 Jun 1992. 3.1 mi W of Tule Well on Camino del Diablo, 5 Mar 1995, *Rebman 2885* (DES).

TA: Borrego Canyon, 3 Feb 1990, *Felger 90-5*. Slopes at Tinajas Altas, 19 Mar 1998, *Felger* (observation). †Butler Mts, spines, seeds, 3820 to 11,250 ybp (5 samples). †Tinajas Altas, seeds, 4010 to 10,070 ybp (10 samples).

Ferocactus emoryi (Engelmann) Orcutt, Cactography 1926 (1): 5, 1926.
[*Echinocactus emoryi* Engelmann, Proc. Amer. Acad. Arts 3: 275, 1856, "Lower Colorado, and principally in Sonora." *Ferocactus covillei* Britton & Rose, Cactaceae 3: 132–133, f. 138–139, 1922, "Sonora, hills and mesas near Altar," 11 Aug 1884, *C.G. Pringle s.n.* (F). *Ferocactus emoryi* subsp. *covillei* (Britton & Rose) D.R. Hunt & Dimmitt, Cact. Syst. Initiat. 20: 16, 2005 (basionym not cited, and name re-published in Cact. Syst. Initiat. 21: 11, 2006)]
Emory barrel cactus, strawberry barrel. Figure 19.

Plants 0.6–1.7 m tall, the stem often 30+ cm diameter, with 21 ribs. Spines all rigid and stout (bristle-like spines not present); central spines 5.5–9.5 cm long (not including curve), hooked on smaller, immature plants and curved but not hooked on mature plants. Flowers often 7.5 cm wide; inner tepals, filaments, style, and stigmas red to red-orange; stigma 16-lobed. Seeds conspicuously pitted. Flower buds produced beginning in early March and flowering (July) August to mid-September; flowers highly fragrant.

Scattered on rocky slopes of hills and mountains, middle to upper bajadas, and occasionally on lower bajadas, plains, and sandy flats. Eastern part of Cabeza Prieta in the Agua Dulce and

Growler Mountains and widespread across Organ Pipe including the Ajo Mountains to higher elevations. It has a 3500-year history in Organ Pipe.

Southwestern Arizona and western Sonora southward to the coastal Yaqui lands southeast of Guaymas, and reported to extend southward to northwestern Sinaloa in the vicinity of Topolobampo (Taylor 1984; Unger 1992).

There are two color-specific populations: a red-flowered northern population and a yellow-flowered southern population. The northern race, in the Sonoran Desert north of Hermosillo and Bahía Kino, Sonora, to southern Arizona, predictably has red to red-orange flowers. The southern race, from the Guaymas–San Carlos region at the southern edge of the Sonoran Desert and southward

Figure 19. *Ferocactus emoryi*. (A & B) Ajo, 31 Jul 2013. (C) N of Bates Mts, 11 Sep 2013. (D & E) Alamo Canyon, Ajo Mts, 5 Nov 2013. (F) Juvenile plant, Javelina Mtn, Sand Tank Mts, 5 Mar 2005.

in Sonora in thornscrub, predictably has bright yellow flowers. The population bridging the northern and southern race, in the Sierra Libre, between Guaymas and Hermosillo, has the full span of yellow, orange, orange-red, or red flowers, and all three colors sometimes occur even on a single plant (Paredes et al. 2000). The southern, yellow-flowered population has been named *F. emoryi* subsp. *covillei* (Britton & Rose) D.R. Hunt & Dimmitt. The type locality for *F. covillei* Britton & Rose, however, is in northwestern Sonora, in midst of the range of the red-flowered, northern population. Hunt and Dimmitt's subsp. *covillei* therefore does not match the definition of having a separate range for a subspecies. According to the prevailing definition, a subspecies is recognized by having a separate range, i.e., separate from the proposed nominate subspecies.

Felger and Zimmerman (2000) disagreed with Taylor (1984) that *F. rectispinus* (Engelmann ex J.M. Coulter) Britton & Rose should be treated as a variety of *F. emoryi*. *Ferocactus rectispinus*, endemic to Baja California Sur, is morphologically and geographically clearly isolated from *F. emoryi*. The basionym, published in 1896 as *Echinocactus emoryi* var. *rectispinus* Engelmann ex J.M. Coulter, shows that Taylor was not the first to make an association of the two species, although neither Engelmann nor Coulter saw the plants in the field (see Lindsay 1955, 1996).

OP: Quitobaquito, *Nichol 28 Apr 1939* (ORPI). E of Bates Well, 4 Mar 1940, *Benson 9896*. Twin Peaks, 3 Dec 1989, *Pinkava 14371* (ASU). Observations, *Felger*: W of Hwy 85 at N boundary of Monument, 23 May 1991; Trail from The Cones to Mount Ajo, 4090 ft, 10 Apr 2005. †Puerto Blanco Mts, on ridge, spines, seeds, modern (30) to 3480 ybp (8 samples).

CP: 7 mi E of Papago Well, 14 Mar 1937, *Harbison 16849* (SD). Bajada, near wash, 19 Mar 1975, *Lehto L18392* (ASU). Observations, *Felger*: Adobe Windmill, W end of Agua Dulce Mts, S side of Growler Pass, 12 & 13 Jun 1992; Childs Mt, 2400 ft, 18 Aug 1992.

Ferocactus wislizeni (Engelmann) Britton & Rose
[*F. wislizeni* subsp. *ajoensis* Fencl & Kalas, Bradleya 31: 7–11, f. 3–6, 8–11, 2013]
Compass barrel cactus, fishhook barrel cactus. Figure 20.

Plants mostly less than 1 m tall, some reaching 1.5 m, the stem very thick, often 35–65 cm diameter; stem ribs often 21–27. Larger plants usually conspicuously leaning (growing) southward. Spines dull gray, the larger spines strongly hooked, longest central spines of adult plants (from curve of hook to base) 6–8.5 cm; outer radial spines slender and bristle-like. Younger plants to about 15 cm tall have markedly longer spines than larger, adult plants; longest central spines often reaching 12 cm. Extrafloral nectaries prominent in the proximal (adaxial) portion of young areoles and actively tended by ants all year. Flowers often 7–8 × 5–7 cm, exceeding the spines, yellow-orange to red-orange, or yellow overall, the inner tepals with an orange-red to red midstripe grading to yellow-orange to yellow on margins, or sometimes the inner tepals bright yellow (all colors between yellow and red-orange are common, including plants next to each other). Filaments pink to red. Seeds essentially smooth with only a slightly raised reticulate pattern. Ants often carry away seeds from hollowed but still fleshy, yellow fruits. Flower buds produced from early March and flowering generally in (late July) August and September; flowers highly fragrant.

Widely scattered in Organ Pipe on sandy gravelly soils of desert plains, lower alluvial flats, and lower to middle bajadas, and thinly and unevenly scattered across much of Cabeza Prieta, mostly valley floors on sandy soils. We have not found this cactus westward from the southern end of the Sierra Pinta in Cabeza Prieta with exception of a single plant at the southeastern corner of the Tinajas Altas region. Soil erosion commonly undermines larger, older plants, especially when growing along the margins of small washes, causing them to topple over and eventually perish. Javelinas sometimes push over the plants and then get into the plant from the bottom to eat the pulp. Sue Rutman says the pulp of this barrel cactus tastes like a cross between a potato and cucumber. This cactus has been in Organ Pipe for at least 10,500 years.

Southwestern and central Arizona to western Texas and adjacent Chihuahua and northern Sonora.

The mutualistic relationships involving ants and the extrafloral nectaries of this barrel cactus has been the subject of extensive ecological investigations, most notably beginning with the work of Judith Bronstein, her lab at the University of Arizona, and colleagues (e.g., Ness et al. 2006; also see *Ferocactus* generic description above).

We find no infraspecific taxon of *F. wislizeni* worthy of recognition. Fencl and Kalas (2013) described the western populations as subspecies *ajoensis*. Their slender forms of the western populations represent the sort of random morphological variation that, if recognized, would lead to a plethora of subspecific taxa. They state that subspecies *ajoensis* has denser spination and larger spines than subsp. *wislizeni*. There may be a trend of larger and stouter spines westward across the species range, but the examples shown for subsp. *ajoensis* appear to be young plants that characteristically have larger and stouter spines than older, larger plants. The authors also state that the flowers are red to orange in subsp. *ajoensis* and yellow in subsp. *wislizeni*. Both flower colors, however, are common across the west–east range of the species.

Felger and Zimmerman (2000: 211) report: "Contrary to a statement by Taylor (1984: 34), we find no evidence that *F. wislizeni* in the southern part of its range . . . intergrades with" the related *F. herrerae* J.G. Ortega. Taylor's statement, however, is from George Lindsay's dissertation (1955; reprinted in Lindsay 1996). There is an eco-geographic gap of perhaps more than 200 km between the southernmost population of *F. wislizeni* in northern Sonora and the northernmost *F. herrerae* in the vicinity of Guaymas, Sonora. Although Taylor and Clark (1983) found little difference in the seeds, the several vegetative differences are conspicuous and consistent. *Ferocactus herrerae* occurs primarily in coastal thornscrub of southwestern Sonora and Sinaloa. In comparison to *F. wislizeni*, *F. herrerae* grows spectacularly fast in cultivation. We also consider *F. tiburonensis* (G.E. Lindsay) Backeberg (*F. wislizeni* var. *tiburonensis* G.E. Lindsay) on Isla Tiburón and the Sonora coast to be a distinct species. *Ferocactus tiburonensis* and *F. wislizeni* are clearly allopatric with no known plants with intermediate morphology (Felger & Wilder 2012).

Ferocactus wislizeni is locally distinguished from *F. cylindraceus* in part by its relatively dull gray, strongly hooked spines, much thicker stems, and general tendency to lean (grow) southward. Zimmerman and Parfitt (2003b) report that claims of hybrids between *F. cylindraceus* and *F. wislizeni* are not substantiated. *Ferocactus cylindraceus* and *F. wislizeni* generally occupy different habitats and are only occasionally found growing together in Arizona beyond our flora area (see *F. cylindraceus*). *Ferocactus wislizeni* occasionally grows with *F. emoryi,* although they generally occupy different habitats. Both species have similar-appearing flowers and may flower at the same time, although in the flora area *F. wislizeni* mostly has orange to orange-red or yellow flowers and *F. emoryi* has deeper red flowers; the spination, however, is clearly distinctive in *F. emoryi*.

OP: Walls Well, *Nichol 2 May 1939* (ORPI). Sandy soil, Growler Mts near Bates Well, 4 Mar 1940, *Benson 9895*. Quitobaquito, 14 Sep 1988, *Felger 88-444*. Hocker Well, 3 Dec 1990, *Felger* (observation). †Puerto Blanco Mts, on ridge, spines, seeds, 3480 to 10,540 ybp (5 samples).

CP: 7 mi E of Papago Well, 20 Mar 1937, *Harbison 16847* (SD). Observations *Felger*: Between San Cristobal Wash and Agua Dulce Mts, 31 Jan 1992; Sand over lava in the Pinacate flow, with *Larrea*, near O'Neill's Grave; Papago Well, 31 Jan 1992; Near Salt Well, 12 Jun 1992.

Figure 20. *Ferocactus wislizeni*. Why: (A) 20 Aug 2006; (E) Why, 8 Aug 2013. (B) Bates Well Road, Organ Pipe, 29 Feb 2008. (C) Gunsight Hills near Hwy 85, 17 Oct 2013; (D) Gachado line camp, 20 Aug 2006. Armenta Ranch Rd near Hwy 85: (F) 17 Oct 2013; (G) 2 Aug 2013. (H) Central spine, Crater Range E of Hwy 85, 7 Jan 2014; (I) Ant (*Crematogastor opuntiae*) visiting extrafloral nectary, Tumamoc Hill, Tucson, 4 Apr 2003, photo by William G. Wilson.

TA: About 2.5 mil SE of Tinajas Altas, Lechuguilla Valley floor near the head of Coyote Wash, 1065 ft, 1 Apr 2011, *Pete Sundt*, observation, from Sundt's vegetation survey plot; species list from the plot, in decreasing abundance: *Ambrosia dumosa, Larrea divaricata, Prosopis glandulosa, Grusonia wrightiana, Lycium fremontii, L. macrodon, L. parishii*, *Carnegiea gigantea, Encelia farinosa, Echinocactus polycephalus, Hilaria rigida, Asclepias subulata*, and one lonely *Ferocactus wislizeni* (see Felger et al. 2012 for description of the habitat and flora).

Grusonia – Club cholla, dog cholla; *perrito*

Low-growing opuntioid cacti forming colonial colonies, the stems more or less cylindrical-club-shaped, upright, rounded in cross-section but with prominent tubercles, remaining green all year. Stem segments (joints) firmly attached and separable only by tearing the woody axis. Stem and floral areoles each with one small, deciduous tubular-conical leaf; areoles with spines and usually with at least some glochids, sometimes absent in older stems, especially in *G. wrighitiana*; spines whitish to gray (reddish or salmon-color when first developing), the larger spines very sharp, rigid, flattened with razor-like margins, mostly pointing downward; spines with a minute and soon-deciduous spine sheath only at the tip of young spines. Flowers one to several at stem tips; outer tepals reddish or pink, the inner and larger tepals whitish or pale yellow. Filaments green, especially near their bases; anthers white to pale yellow. Fruits fleshy, greenish or yellow when ripe and usually soon drying. (The fruits seem to dry sooner during drought conditions than during times of higher soil moisture.)

Grusonia includes 15 species in southwestern USA and Mexico. Four species occur in Arizona (figure 21). As explained below, we consider the club cholla in the flora area previously called *Grusonia kunzei* (e.g., Felger & Zimmerman 2000; Pinkava 1999b, 2003b) to be *G. wrightiana* and the one previously called *G. parishii* in the flora area to be *G. kunzei*.

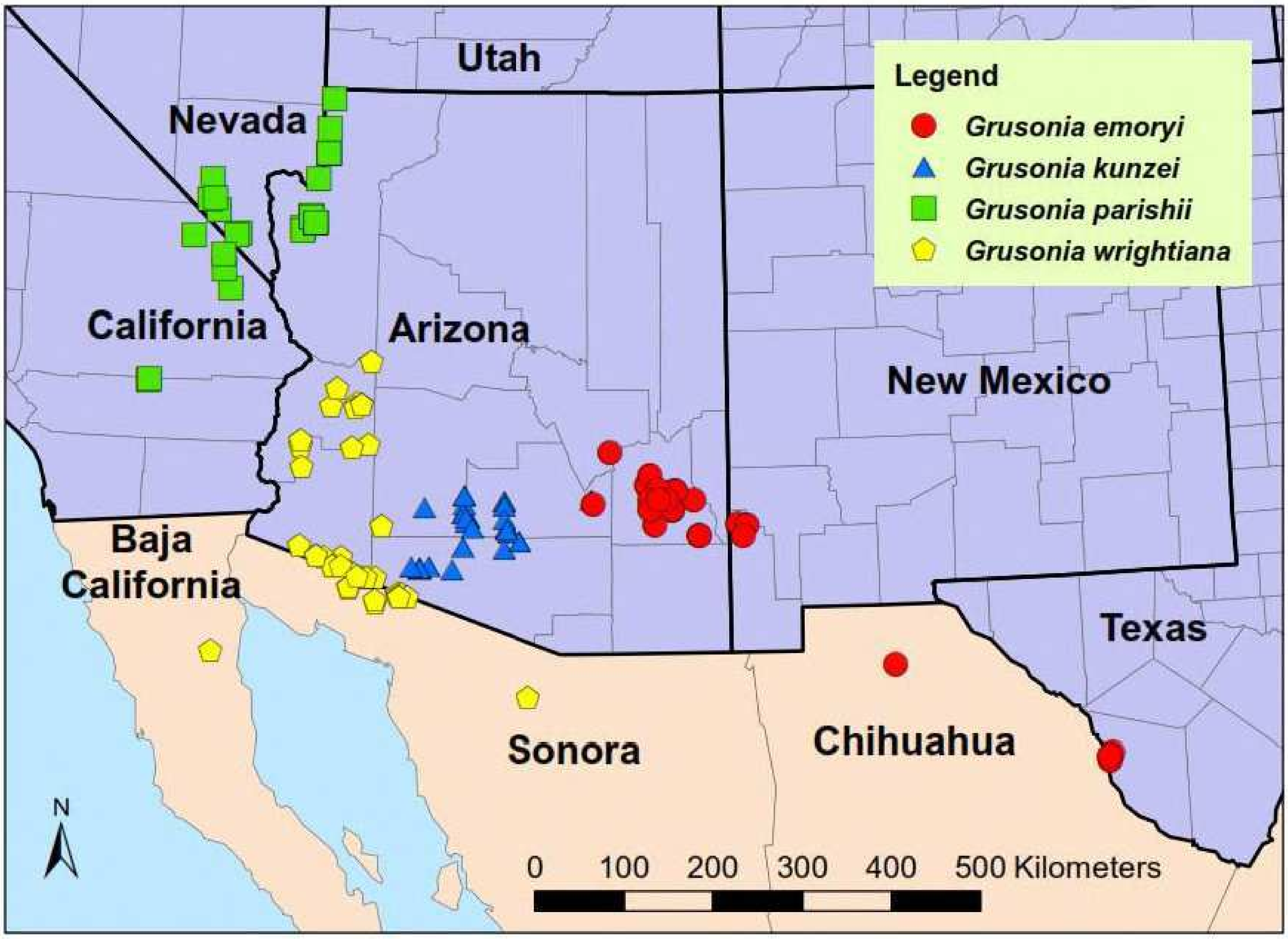

Figure 21. Specimen-based distribution of the four Arizona *Grusonia* species. Map by Marc Baker.

Some authors maintain that *Grusonia* and *Corynopuntia* are both valid and separate genera but, thus far, data supporting this viewpoint are inconclusive. Although *G. bradtiana* (J.M. Coulter) Britton & Rose, the type species for the genus, compared to other *Grusonia* is unusual with respect to some of its morphological and genetic attributes, it seems rather extreme to include *G. bradtiana* under its own monotypic genus.

Spine glands as extrafloral nectaries (EFNs) are documented for a number of *Grusonia* species. Michele Lanan (pers. com. to Felger, 21 May 2014) found that *G. emoryi* secretes tiny amounts of liquid from the ends of tiny developing spines on new growth, which is consistently collected by the dark rover ant (*Brachymyrmex patagonicus*) (figure 22), and once the spines grow larger they seem to stop secreting. Researchers have found EFNs on *Grusonia emoryi, G. invicta*, and *G. wrightiana* growing on the grounds of the Arizona-Sonora Desert Museum in Tucson (Marazzi et al., unpublished manuscript, and Joshua Ness, pers. com. to Felger, 21 May 2014). Marc Baker (6 Aug 2013) observed small black ants (probably *Brachymyrmex*) on the buds of *G. schottii* cultivated in Chino Valley, AZ. The ants were stroking the young spines with their various appendages. There was no reaction when Benedict's Reagent was applied to the areoles indicating the absence of simple sugars, while the same reagent applied to the areoles of young stems of *Cylindropuntia acanthocarpa* and *C. imbricata* stained the short hairs of the areoles orange-yellow. The ants on *G. schottii* may have simply been exploring or were obtaining nutrients other than simple sugars, or, as suggested by Michele Lanan (pers. com. to Felger, 21 May 2014), it might be that the ants were so efficient at removing the tiny amount of liquid that there was nothing left for the Benedict's reaction. Although "ants don't play" (Hölldobler & Wilson 1990: 370), biologists do.

1. Stems often 10–20 cm tall, formed of 1–3 joint(s); new branches arising from near ground level to over half way up stem; spines generally fewer than 15 per areole, the larger spines 2.2–4 cm long; fruits with glochids only. .... **Grusonia kunzei**
1. Stems often 30–50 cm tall, formed of 2–6 joints; new branches held aloft and well above the ground; spines about 20 per areole, the larger spines 4–4.8 cm long; fruits with stout spines and glochids. .... **Grusonia wrightiana**

Figure 22. *Grusonia emoryi*. Plant cultivated in Tucson, grown from a piece broken off by an off-roader at 32°47'25.66"N, 110°40'13.10"W, Route 77 north of Mammoth on a power line access road, Feb 2009, Pinal Co.: (A) nectar droplet on a spine-gland; (B) *Brachymyrmex* collecting nectar; photos by Michele Lanan, 21 May 2014.

Grusonia kunzei (Rose) Pinkava, J. Arizona-Nevada Acad. Sci. 32 (1): 50, 1999.
[*Opuntia kunzei* Rose, Smithsonian Misc. Collect. 50 (4): 505–506, 1908. *O. stanlyi* Engelmann ex B.D. Jackson var. *kunzei* (Rose) L.D. Benson, Proc. Calif. Acad. Sci., ser. 4, 25: 248, 1944. *Corynopuntia kunzei* (Rose) M.P. Griffith, Haseltonia 9: 91, (2003)].
Desert club cholla, devil cholla. Figure 23.

Low-growing club chollas often forming colonies 0.8–2 (5+) m across. Stem segments 1–3 per stem, clavate to elongate and tapering at both ends, erect, 5–13 cm long, generally 4–5 time longer than wide, with prominent tubercles 1.2–2.5 cm long. Spines very sharp, newly emerging spines pinkish, reddish, or reddish orange, becoming whitish to gray; the larger spines (upper centrals) mostly pointing downward, (2.2) 2.5–3.5 (5.8) cm long, and 1.2–1.8 mm wide and 0.5–1 mm thick at base. Flowers terminal, often several per stem, outer tepals yellow with salmon-pink midstripe extending into a long tooth, the inner tepals to about 2 cm long, pale yellow with some green at the base. Filaments greenish below and pale yellow above; anthers pale yellow. Fruits about 3.5–5 cm long, fleshy and yellow when ripe and usually soon becoming dry, with glochids but not spines; sometimes proliferating with a second fruit. Flowering in June and July, the flowers open in the late morning. Fruits ripening in late summer. $2n = 22$.

South-central Arizona in Arizona Upland of the Sonoran Desert, including the north-central and northeastern part of Organ Pipe. *Grusonia kunzei* in Organ Pipe occurs in localized but substantial colonies or assemblages of colonies on gravelly desert flats of gently sloping bajadas with sandy loams. Often growing with *Ambrosia dumosa*, *A. deltoidea*, *Carnegiea gigantea, Cylindropuntia acanthocarpa*, *C. fulgida*, *C. leptocaulis*, *Echinocereus engelmannii*, *Larrea divaricata*, *Mammillaria grahamii*, *Olneya tesota*, and *Parkinsonia microphylla*.

Grusonia kunzei most resembles *G. parishii* (Orcutt) Pinkava, which has wider upper central spines (to 3 mm), shorter tubercles, stem segments that are generally obovoid, and very low, trailing branches. *Grusonia parishii* occurs in the Mojave Desert in northwestern Arizona, California, and Nevada. Pinkava (1999b, 2003b) placed populations of what we now consider to be *G. kunzei* under *G. parishii* based on the low stature, $2n = 22$ chromosome number, and spineless fruits.

Although correctly classified by Benson in his first and second editions of *The Cacti of Arizona* (Benson 1940, 1950), he jumbled the taxonomy in his third edition (Benson 1969), which he carried over to his treatment of the cacti of the United States and Canada (Benson 1982). In these later works he erroneously placed populations of *Grusonia wrightiana* under the name *Opuntia stanlyi* var. *kunzei*, although the lectotype he chose had a spineless fruit (a feature of the actual *G. kunzei*, but not *G. wrightiana*). One factor that contributed to Benson's error was his confusion over the mileages given by Dr. R.E. Kunze for his locality data for his original (type) collection of *Opuntia kunzei*. Kunze stated in his correspondence to Rose that he found the plant 40 miles (the lectotype label, quoted below, has 26 miles) south of the Copper Mine (the present-day town of Ajo) and 25 to 35 miles north of the Mexican boundary. Benson (1982: 917) noted that, "the mileage figures do not check," probably with the assumption that Kunze went south from Ajo en route to the more recent border crossing at Lukeville. Kunze, however, stated that he traveled on the eastern slope of Gunsight Mountain Range (Gunsight Hills and Pozo Redondo Mountains), which indicates that he was along the well-established route at the time to Tucson via the Quijotoa Valley or possibly farther east (figure 21). Following this route, the mileages do check. In addition, Kunze said that "immense tracts between smaller arroyos were covered with this species." There are no such tracts of *Grusonia* between Ajo and Lukeville, but there are in the plains east of the Gunsight Hills. Pinkava (1999b, 2003b) followed Benson's error but was the first to note the problem of the spineless fruit on the lectotype, which he discovered after his treatments were published (Donald Pinkava, pers. comm. to Baker, 2012). Furthermore, we now know that the larger, lower-elevation and Lower Colorado

Valley species, *G. wrightiana*, does not occur east of the Gunsight Hills, east of Organ Pipe Cactus National Monument.

OP: Grass Canyon, NE corner of Monument, 17 Feb 1962, *Steenbergh 2-1761-1* (ORPI). 0.9 mi on Hwy 85 south of N boundary of Monument, gently sloping bajada, gravel and silt, *Cercidium microphyllum, Larrea* sp., *Ambrosia dumosa, A. deltoidea, Opuntia fulgida, O. acanthocarpa* var. *major*, *Echinocereus engelmannii, Mammillaria grahamii*, 22 Mar 1988, *Felger 88-110* (ARIZ, ASU). N boundary of monument, 0.2 km W of AZ Hwy 84, *Acourtia wrightii, Ambrosia deltoidea, A. dumosa, Bouteloua aristidoides, B. barbata, Carnegiea gigantea, Celtis pallida, Echinocereus engelmannii var. acicularis, Eragrostis cilianensis, Ferocactus emoryi*

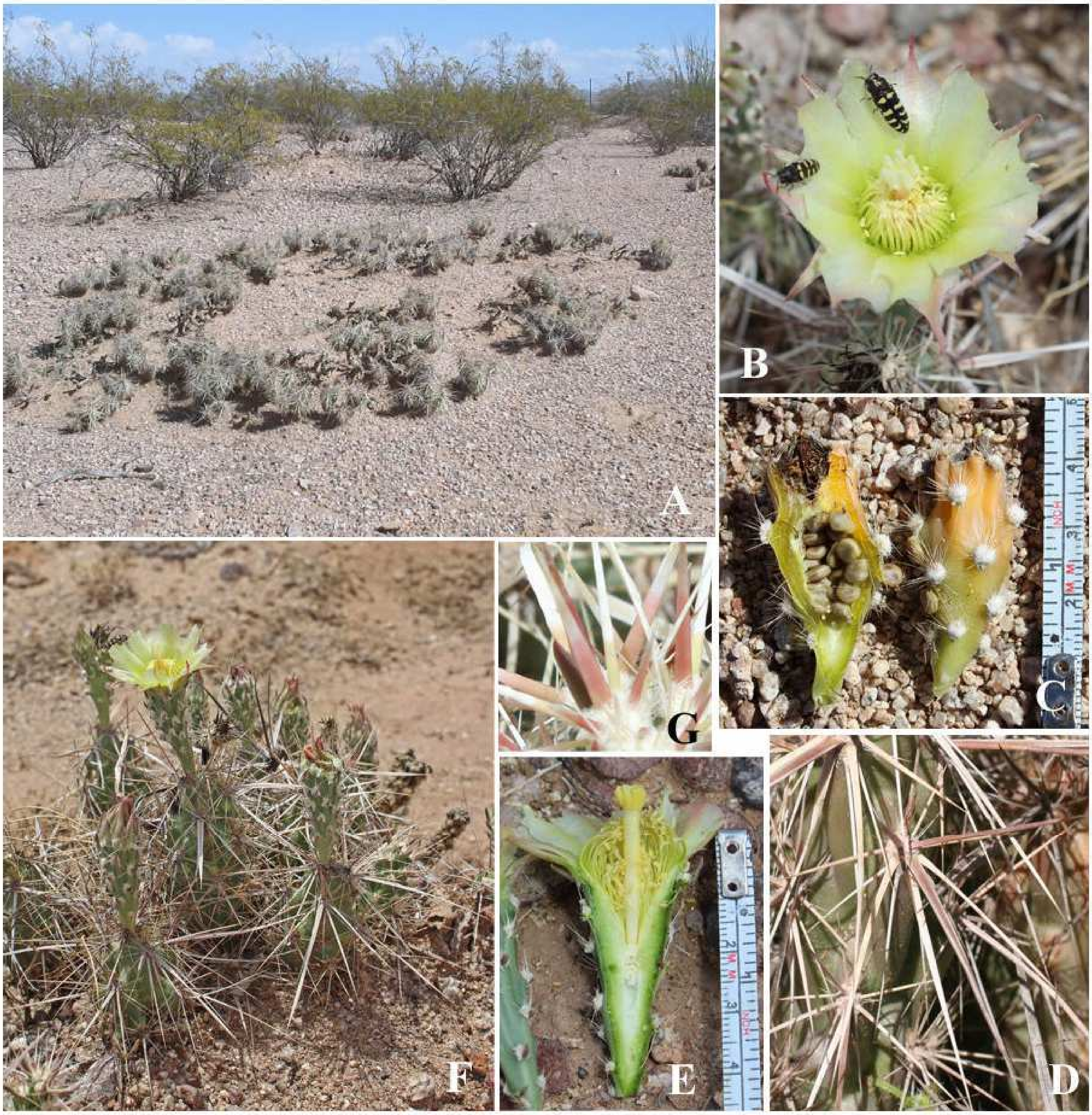

Figure 23. *Grusonia kunzei*. (A) Clonal colony, N boundary of Organ Pipe, W of Hwy 85, 10 Oct 2004. Hwy 85 near Armenta Ranch Road: (B) buprestid beetles, *Acmaeodera* sp., 31 Jul 2013; (C) 20 Oct 2013; (E) 31 Jul 2013; (F & G) plant and young, emerging spines, 31 Jul 2013. (D) N of Kuakatch Wash, E of Hwy 85, 13 Mar 2010.

(rare), *Hilaria rigida, Krameria grayi, Larrea divaricata, Leptochloa filiformis, Mammillaria grahamii, Muhlenbergia porteri, Olneya tesota, Opuntia acanthocarpa, O. engelmannii var. leptocaulis, Peniocereus greggii* (rare), *Sporobolus cryptandrus,* 2 Dec 1990, *Felger 90-500* (ARIZ, ASU, DES). Vicinity of Walls Well, NE boundary of Monument, 19 Nov 2001, *Felger* (observation). 100 m SW of Hwy 85 and Armenta Ranch Road, *Rutman 31 Jul 2003.*

Pima County: "*Opuntia kunzei* Rose, sp. nov., twenty-six m. south of the Copper Mine, 04.603, 1904, *R.E. Kunze*" (lectotype of *Opuntia kunzei*, fruit on right side of sheet, US 535063 [Rose's type specimen of *Opuntia kunzei* includes Kunz collections from two different dates and two different places; therefore Lyman Benson (1982) chose the fruit on the right side of the herbarium sheet, with glochids but devoid of spines, as the lectotype.]).

Grusonia wrightiana (E.M. Baxter) E.M. Baxter, Calif. Cactus 58, 1935
[*Opuntia wrightiana* E.M. Baxter, Cactus & Succ. Jour. 4: 283, 1932 ("description meager but valid," Benson 1982: 917). *O. wrightiana* (E.M. Baxter) Peebles, Desert Pl. Life 9: 45, 1937. *O. stanlyi* Engelmann var. *wrightiana* L.D. Benson, Proc. Calif. Acad. Sci., ser. 4, 25: 248, 1944. *O. kunzei* var. *wrightiana* (E.M. Baxter) Peebles, Leafl. W. Bot. 5 (12): 192, 1949. *O. stanlyi* Engelmann var. *peeblesiana* L.D. Benson, Cacti Ariz. ed. 3, 20, 64, 1969. *Corynopuntia stanlyi* (Engelmann) Knuth var. *wrightiana* Backeberg, Cactaceae 1: 360, 1958]
Devil club cholla. Figure 24.

Cholla-like plants forming colonies often (0.5) 1–3.5 m wide. Branches often 30–57 cm tall, erect, stout, and tough, branching mostly from near base of plant, but with new branches held aloft and often branching from 6–10 cm above ground level. Stem segments 2–6 per stem, the larger stem segments 8.5–16 × 3.3–4.8 cm, more or less cylindroid with elongated, prominent tubercles. Spines stout, very sharp and rigid, about 20–30 per areole, most of the larger ones deflexed downward. Larger spines 4–5 cm × 1.5–2 mm maximum width, scabrous with minute transverse ridges, flattened or diamond-shaped in cross section; smaller spines terete; glochids few in upper part of areoles, or absent. Leaves to about 1 cm long, mostly red, and quickly deciduous.

Flowers 4.5–5.5 cm wide. Inner tepals pale yellow or cream colored, 25–3.5 cm long with a reddish central stripe; outer tepals pinkish, rather thick with thickened reddish tips, grading into the terete, reddish, and reduced pericarpel leaves. Filaments green basally, cream-white to yellow distally; anthers pale yellow. Stigma cream colored. Fertile fruits 4.5–8 × 2.4–3 cm, separating relatively easily from the stems, fleshy, obovoid, the pulp yellowish, the skin dull yellow, the areoles with spine clusters and glochids; floral remnants persistent. Sterile fruits often present, with floral remnants but without seeds, usually cylindroid (more narrowly cylindroid than the fertile fruits), remaining green, and more firmly attached to the stems than the seed-bearing fruits. Seeds 3.3–5 mm long, light tan, smooth. Flowering April, May and June; ripe fruits seen from late August until the following May. As the fleshy, yellow fruits ripen, almost all of them (at least during dry years) are chewed open on one side, presumably by small mammals and/or perhaps by birds and the seeds removed.

Common in the Lower Colorado Valley region of the flora area, on sandy flats along the southwestern margin of Organ Pipe and across much of Cabeza Prieta on valley flats and low hills; sandy or silty soils, often with *Larrea* on low sand hummocks (the hummocks seem to form as a result of sand trapped by the cactus colony) and less often on pavements and rocky slopes. Especially abundant on sand flats and low, stabilized dunes in the south-central and southwestern part of Cabeza Prieta and occasional in the Lechuguilla Valley east of Tinajas Altas.

Northwestern Sonora from the Pinacate Region southward near the coast to Bahía San Jorge (vicinity of 31° 10' N) and eastward to Tubutama (vicinity of 30° 53' N, 111° 27' W), northeastern Baja California in the San Felipe Desert, and southwestern Arizona in western Pima County, and

Yuma and La Paz Counties (figure 21). Lyman Benson (1982: 365) tells that this club cholla "in California was reported by Baxter (1932, 1935), and the report was accepted by Wiggins (1963). . . [and although it] . . . does occur just east of the Colorado River in Yuma Co., Arizona, no specimens from across the river in California have been seen." Marc Baker and Michelle Cloud-Hughes searched for it on several occasions in potential habitat in California but did not find it there.

OP: Quitobaquito, Jan 1894, *Mearns 2735* (CAS). Quitobaquito, 27 Nov 1939, *Harbison 26175*. Quitobaquito, 5 Mar 1940, *Peebles 14561*. 6 mi E of Quitobaquito [based on data from Lehto's notebooks], 24 Oct 1965, *Lehto 5489-b* (ASU). 1 mi NW of Border Monument 180, T15S, R12W, 700 ft, low sand dunes, 10 Apr 1978, *Lehto L-22481* (ASU). 0.9 mi E of Aguajita Spring, *Atriplex polycarpa*, *Ambrosia dumosa*, *Suaeda*

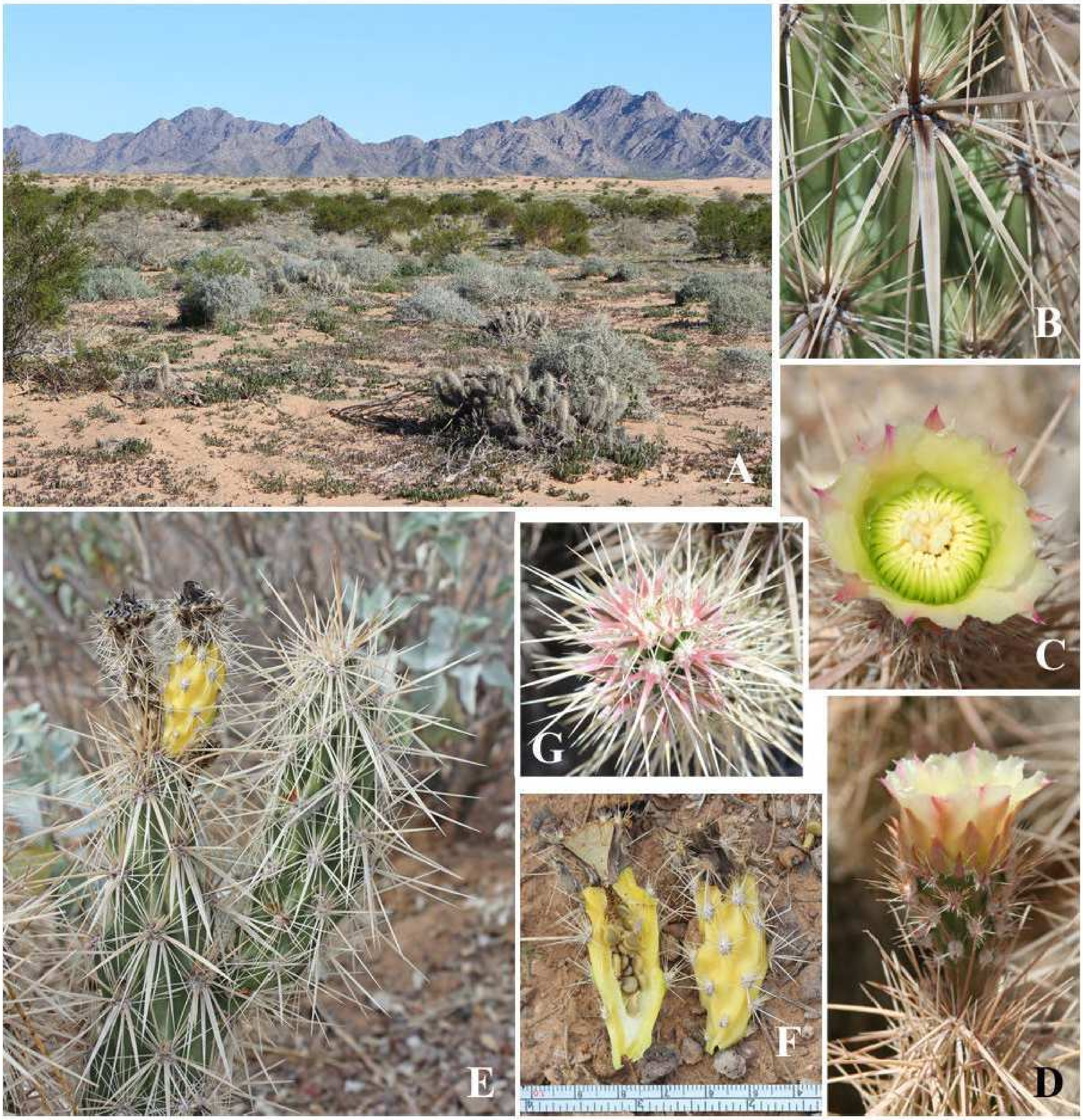

Figure 24. *Grusonia wrightiana*. (A) Pinta Sands, 11 Feb 2014. La Abra Plain at U.S./Mexico boundary: (B) Sonora, 26 Aug 2013; (C & D) Organ Pipe, 22 Jun 2006; (G) young, emerging spines, Sonora, 26 Aug 2013. (E & F) Garden in Why, 4 Jan 2014.

moquinii, Larrea, Echinocereus engelmannii, Ferocactus emoryi, 6 Apr 1988, *Felger 88-324* (ASU). 0.9 mi W of Quitobaquito (at old fields below pond) on border road, sandy-gravelly soil of low hills and flats, *Atriplex polycarpa, Carnegiea gigantea, Fouquieria splendens, Olneya tesota, Opuntia acanthocarpa, Ambrosia dumosa, Mammillaria thornberi, Proboscidea altheifolia*, 14 Sep 1988, *Felger 88-469*. Aguajita Wash, very fine loam, *Atriplex polycarpa* flat, *Atriplex polycarpa, A. linearis, Atamisquea, Larrea, Prosopis, Lycium*, 13 May 1988, *n* = 22, *Baker 7613* (ASU). 0.4 mi E of Aguajita Wash along Puerto Blanco Drive, sandy flat with *Atriplex polycarpa, Larrea*, 19 Jun 1989, *Felger 89-231*. Hocker Well, 3 Dec 1990, *Felger* (observation).

CP: Papago Wells, 1 Mar 1939, *Nichol 1 Mar 1939*. 1 mi NW of Border Monument #180, 700 ft, low dunes, 10 Apr 1978, *Lehto L-22481* (ASU). Tule Well, sandy flat and wash, saline soil, 6 Apr 1979, *Lehto L-23567* (ASU). Between Half Way Tank and Buck Peak Tank, 14 Jun 1992, *Felger 92-607*. 1.7 mi on Camino del Diablo E of W border of Refuge, 16 Jun 1992, *Felger* (observation). 7 mi W of O'Neill's grave, sand flats including *Larrea, Hilaria rigida*, few *Carnegiea, Echinocereus engelmannii*, few *Ferocactus wislizeni*, 15 Sep 1992, *Felger 92-784*. 24.5 mi SW of Cabeza Prieta boundary with Organ Pipe, Camino del Diablo en route to Pinta Sands, 32°05'N, 113°28'W, sandy soil, with *Opuntia ramosissima, Echinocereus engelmannii, Ferocactus* sp., *Carnegiea*, etc., 4 Mar 1995, *Rebman 2880* (ASU, DES, UCR). Just W of Pinacate Lava Flow, *Larrea tridentata, Ambrosia dumosa*, 7 Apr 2002, *Hodgson 18704* (DES).

TA: Tinajas Altas, 9 Mar 1937, *Harbison 16999 & 17000* (SD). Camino del Diablo, E of Raven Butte, 29 Nov 2001, *Felger* (observation).

Yuma County: Petrified Forest near Colorado River, 4 mi W of Quartzsite-Yuma road, 33 mi N of Yuma, *Allan B. Clayton 15 Apr 1934* (holotype of *Grusonia wrightiana*, DS 691434 [CAS]).

Lophocereus

This genus includes three species. *Lophocereus gatesii* M.E. Jones occurs in southern Baja California Sur and *Lophocereus marginatus* (de Candolle) S. Arias & Terrazas (*Pachycereus marginatus* (de Candolle) Britton & Rose) occurs in south-central Mexico (Arias & Terrazas 2009).

Lophocereus schottii (Engelmann) Britton & Rose var. **schottii**
[*Cereus schottii* Engelmann. *Pachycereus schottii* (Engelmann) D.R. Hunt]
Senita; *sinita, músaro*; ce:m ĭ. Figure 25.

Many-stemmed columnar cacti, often 2–4 (7) m tall branching mostly at or near the base of the plant, often forming clonal colonies (Parker 1989). Stem tissue becoming black on cut surfaces (also see *Carnegiea* and *Cylindropuntia fulgida*). Stems strongly dimorphic—as the stems elongate, usually after reaching more than about 1.5 m in height, they become more slender, much less fleshy, and the number of stem ribs increases. Lower portion of stems, sterile (not producing flowers), with 5 stem ribs, relatively thick, the larger stems often (8.5) 14–16 cm diameter, the areoles widely spaced and the spines often 5–7 mm long, stout and rigid, not markedly twisted, and with enlarged bases. Upper part of the stems fertile (producing flowers), with 5–7 stem ribs, relatively slender, often 5.5–10 cm diameter, the areoles close together to essentially contiguous, and bearing a dense, shaggy covering of long, slender, twisted, and often flattened spines 4–10 cm long, these spines obscuring the stem surface.

Fertile areoles multiple-flowered (*Myrtillocactus* of Mexico is one of the few other genera of cactus producing more than 1 flower per areole). Flowers nocturnal, 2.5–4 × 3.8–4.2+ cm; weakly bilaterally symmetrical (the tube slightly curved upward, the style lying near the lower side of the tube). Inner tepals whitish to pinkish, spreading open early in the evening (e.g., 8 p.m. on a hot, mid-August night) and becoming recurved before sunrise. The flowers open shortly after sunset and close before or soon after dawn, although the flowers stay open longer in cooler weather, and on cool spring days they may remain open nearly all day. (In Sonora, Richard found that flowers open when a flowering stem is taken from midday summer heat to an air-conditioned room). Filaments, style, and stigmas white, the anthers cream colored. Flowering and fruiting mostly through the hotter months: flowers recorded March–December, but mostly April–September; fruits April–December, peak fruiting often in June. Fruits ovoid to globose, 2–4 cm diameter, essentially spineless, becoming bright red and edible when ripe, irregularly splitting from the top, the pulp bright red; seeds small and blackish. At peak fruiting during favorable years, the upper stems often are loaded with bright red fruits. The pulp and seeds avidly consumed by birds and carried away by ants, and it is often difficult to find ripe fruits in the morning before the birds and ants have hollowed them out. Seeds blackish (dark red-brown under magnification and strong light), (2.2) 2.4–2.8 × 1.8–2.1 mm, shiny and smooth, with a low ridge.

Locally along the southern border of Organ Pipe, westward from the Santa Rosa Mountains, and most common in Senita Hills and the granitic outwash plain of the Senita Hills in the La Abra Plain (Parker 1989). A spectacular stand of organ pipes, saguaros, and senitas occurs in Lost Cabin Basin near Victoria Mine. Also at a few localities, and rare, in the southern part of Cabeza Prieta. Senitas are more common in nearby areas in Sonora. Their distribution in Arizona and northern Sonora is limited by freezing weather, and presumably the western distribution in northwestern Sonora and western Arizona is limited by drought (e.g., Turner et al. 1995). "Evidence of freeze damage, indicated by callused stem tips with new stems emerging from just below the callus tissue or elsewhere on plants, is widespread among senita populations in Arizona and [nearby] northern Sonora (Felger and Lowe, 1967; Nobel, 1980)" (Parker 1989: 399; similar freeze-damage also is evident on organ pipe plants, *Stenocereus thurberi*). During the extreme drought of the 2000s, widespread and significant mortality of senitas occurred in parts of northwestern Sonora and to a lesser extent in Organ Pipe.

Variety *schottii* is characterized by relatively thick stems, 5–8 stem ribs, and an essentially trunkless, or basitonic, branching habit. This is the northern variety, restricted to the Sonoran Desert in southwestern Arizona and western Sonora, Baja California, and Baja California Sur northward from La Paz. It ranges southward in Sonora to the Guaymas region. Two individual senitas were found in the Chuckwalla Mountains of southeastern California that appear to be wild but are only 0.5 km from what was once a private residence. One of the individuals flowers but does not form fruits, indicating that the species is an obligate outcrosser and that there are no other mature individuals within pollination distance. This is the only population of this cactus in the United States apart from southwestern Arizona (Cloud-Hughes & Baker, accepted for publication).

Variety *schottii* in Sonora is replaced to the south by var. *australis* (K. Brandegee) Borg (var. *tenuis* G.E. Lindsay), which ranges southward from the coastal plains southeast of Guaymas (vicinity of Potam) into northwestern Sinaloa (vicinity of Guasave). A similar scenario occurs in southern Baja California Sur. Variety *australis*, primarily in thornscrub, has relatively slender stems with 6–10 ribs, branches arise at various heights well above the base, and the plants often form short trunks (especially towards the Sinaloan border). Although Lindsay (1963) named the southwestern Sonora plants var. *tenuis*, they appear morphologically indistinguishable from var. *australis*, described by Brandegee (1900) from the Cape Region of Baja California Sur (Felger & Wilder 2012).

In *Lophocereus schottii* there is a great variation in stem size ranging from larger stems with fewer stem ribs (5–7) in the northern Sonoran Desert to smaller and more slender stems with 6–10 ribs in thornscrub in southern Sonora (figure 35 c & d; also see *Peniocereus striatus*). The clinal shift in architecture and morphology, from stems with a higher surface-to-volume ratio in the south to stems with a lower surface-to-volume ratio in the north, is interpreted as an adaptation to increased aridity northward (Felger & Lowe 1967; also see Turner et al. 1995).

Patrolling ants attracted to extra-floral nectaries in the areoles provide protection from herbivorous insects (Turner et al. 1995). "Developing buds, flowers and immature fruits produce extrafloral nectar (EFN) from the tips of tepals, photographs of which can be found in Chamberlain & Holland (2008). In addition to reproductive tissues, *P. schottii* has extrafloral nectaries just below their areoles (sub-areole nectaries), but secretion from them has been largely observed after flowering seasons on new stem growth" (Holland et al. 2009: 90–91). Much like the well-known mutualism between yuccas and yucca moths, there is an obligate relationship between sinita and a pyralid moth, *Upiga virescens* (e.g., Fleming & Holland 1998; Hartman et al. 2002). The female moths collect pollen on specialized abdominal scales and actively deposit pollen on the stigma, and deposit a single egg in each pollinated flower. The larvae feed on sinita ovules, preventing seed set in individual fruits, but enough flowers escape predation to produce significant numbers of fruits and seeds. However, seedling establishment among the northern populations is a rare event and clonal propagation from stems is a more common occurrence.

Figure 25. *Lophocereus schottii*. Senita Basin: (A) 14 Jan 2014; (B) 18 Jun 2012. (C) La Abra Plain, Organ Pipe, 22 Jun 2006. Organ Pipe headquarters: (D) 18 May 2006; (F) 22 May 2006. (E) Immature, or sterile stem tip, Sierra Blanca, Pinacate Biosphere Reserve, 18 Jan 2009.

The name "senita," in common use in Arizona, is a corruption of the Mexican vernacular name "sinita." The fruits are edible but not as sweet and not nearly as large as organ pipe and saguaro fruits (e.g., Betty Melvin in Zepeda 1985: 55). The stems are highly esteemed in Mexico for medicinal purposes, especially stems with five ribs. Considerable quantities are harvested for personal and commercial purposes (e.g., Felger 2000, 2007; Paredes et al. 2000). Five-ribbed stems are the sterile or juvenile growth, and are thicker, "softer" (more flaccid and much juicier), and not as tough as fertile parts of the stem with a higher number of ribs. The 5-ribbed stems are used in remedies for diabetes, stomach ulcers, and cancer, and also as a remedy for falling hair (*evita la caida pelo*) and blood circulation (*circulación de la sangre*). As a common preparation, a cross section of the stem, about 2 cm thick, is cooked in about one liter of water until it boils. This liquid is then drunk through the day as one would drink water (*se pone en un litro de agua hasta hervir, y se toma como agua de diario*). The fresh as well as dried star-shaped cross-sections of stems are widely sold in herbal shops in Mexico, even as far as Mexico City and Tijuana. *Músaro*, derived from the Yoeme (Yaqui) language, is the name often used in Mexico.

OP: Gray's Well [= Blankenship Well at Dos Lomitas], *Nichol 4 May 1939* (ORPI). 1 mi E of Quitobaquito, S slope, gravelly silt, few, 2 Jun 1951, *Blakely 323* (DES). 2.4 mi W of Hwy 85 on Puerto Blanco Drive, 19 Jun 1989, *Felger 89-229*. Dos Lomitas, 13 May 1990, *n* = 11, cited in Madroño 39: 106, 1992 [Pinkava et al. 1992b], *Baker 7831-A* (ASU, ORPI). 1 mi W of Lukeville at international boundary, 18 Nov 1991, *Felger* (observation).

CP: 7 mi E of Papago Well, 14 Mar 1937, *Harbison 17061* (SD). Davidson Canyon (Simmons 1965: photo, 2 Feb 1964). SW side of Agua Dulce Mts, 32°02'N, 113°18'W, sandy flats, about one dozen plants to 7 ft tall, 12 May 1997, *Luke Evans* (observation).

Sonora: Sierra de Sonoyita, and southeast towards Santa Magdalena, *Schott July 1855* (holotype, MO; the protologue says "Sonora, towards Santa Magdalena").

Mammillaria – Fishhook cactus; *cabeza de viejo*

The three species in the flora area are small cacti of unrelated species in this large genus. Stems globose to cylindroid with distinct (separate) tubercles. Tubercles each with a terminal spine-bearing areole and subtending a very reduced, axillary, flower-bearing areole that sometimes also bears a few bristle-like spines. Central spines hooked (those in the flora area). Flowers diurnal and relatively small for the family. Fruits succulent, globose to elongated, smooth (spineless), red. All three of species in the flora area are 2*n* = 22. During the decade preceding 2014, *Mammillaria* plants in the flora area have been dying due to drought and drought-related responses such as increased herbivory.

The genus includes 165 species, mostly in Mexico, some in southwestern USA, and few in the West Indies and Central America.

1. Seeds 1.6–2.4 mm long, the lower ⅓ covered with a light-colored, corky cup-like base, the seed surface reticulate and wrinkled but not pitted (note: dried fruits can often be found below the spine clusters in the tubercle axils); fruits not good to eat. .... **Mammillaria tetrancistra**
1. Seeds slightly less than 1 mm long, without a corky base, the seed surface pitted; fruits good-eating.

  2. Hook of central spine 2–3 mm across; stems commonly 3.5–6 cm wide; stigma green; widespread across the flora area, rocky places and plains.......................... **Mammillaria grahamii**
  2. Hook of central spine 1.5 (2) mm across; stems commonly (2) 3–3.5 cm wide; stigma magenta; lower bajadas and desert flats in Organ Pipe. .... **Mammillaria thornberi**

Mammillaria grahamii Engelmann

[Among the many synonyms are: *M. grahamii* var. *arizonica* Quehl. *M. grahamii* var. *oliviae* (Orcutt) L.D. Benson. *M. microcarpa* (Engelmann) Britton & Rose. *M. milleri* (Britton & Rose)

Bödeker. *M. sheldonii* (Britton & Rose) Bödeker. *M. swinglei* (Britton & Rose) Bödeker]
Arizona fishhook cactus; *cabeza de viejo*; ban 'isvig, ban cekida. Figure 26 A–C.

Stems single (unbranched) or with 1 to several branches; stems globose to cylindroid, 5–15 (30) × 3.5–6.5 cm. Central spines 1–3 per areole, at least 1 of them strongly hooked. Flowers often 2–3.5 cm wide, usually in a ring near the top of the stem. Inner tepals showy, pink to rose purple. Stigma green. Fruits edible. Seeds 0.75–0.95 mm diameter, rounded-obovoid, blackish, and pitted. In southern Arizona several flushes of flowers may be produced annually, each about 5 days after soaking rains (Bowers 2002).

Widespread and common across the flora region including sandy and rocky soils of valley plains, bajadas, and rocky slopes to higher elevations. Plants in granitic mountains tend to have pale spines whereas those in volcanic areas tend to have dark spines. A fishhook cactus resembling this species has been in the flora area for more than 20,000 years. *Mammillaria grahamii* occurs with *M. tetrancistra*, and with *M. thornberi* from Quitobaquito to the nearby Río Sonoyta in Sonora and in the lower Sonoyta Valley in Organ Pipe. Seeds of *M. grahamii* and *M. thornberi* appear to be indistinguishable.

As broadly interpreted, *M. grahamii* ranges from southeastern California to west Texas, northern and western Chihuahua and most of Sonora nearly to the Sinaloa border. Distinguishing varieties or subspecies is problematic. *Mammillaria grahamii* subsp. *sheldonii* (Britton & Rose) D.R. Hunt [*M. swinglei* (Britton & Rose) Bödeker] occurs in coastal Sonora from about Puerto Libertad to the southwestern part of the state. Subspecies *sheldonii* is reported to have smaller and whitish flowers and fewer radial spines (12–15) than subsp. *grahamii* (20–30+), but other than flower color, consistent distinguishing features appear elusive (Felger & Wilder 2012).

Fresh fruits of this species and the less common *M. thornberi* are tasty and were eaten by children and probably by people of all ages as trail snacks (Felger & Moser 1985; Hodgson 2001). Ear drops prepared from the stems served as a treatment for earache for Gila River Pimas and Seris (Curtin 1949; Felger & Moser 1985). Gila River Pimas rubbed the red fruits "on arrowshafts to color them" (Curtin 1949: 57).

OP: Cipriano Well, *Nichol 27 Apr 1939* (ORPI). Bates Well, 5 Mar 1940, *Benson 9945*. Quitobaquito, 29 Mar 1988, *Felger 88-129*. Trail from The Cones to Mount Ajo, 4100 ft, 10 Apr 2005, *Felger* (observation). †*M.* cf. *grahamii*: Alamo Canyon, spines, seeds, 1150 to 14,500 ybp (3 samples). †Montezuma's Head, spines, seeds, 20,490 & 21,840 ybp. †Puerto Blanco Mts, on ridge, spines, seeds, 990 to 7580 ybp (8 samples).

CP: Observations: Sand over lava at E side Pinacate flow, 31 Jan 1992, *Felger*; Senita Tank, 14 Jun 1992, *Felger*.

TA: Granite mountain at NW side of Raven Butte, 30 Dec 2005, *Felger 05-384*. 0.3 mi SE of Tinajas Altas, upper bajada, decomposed granitic rocky soil, 1175 ft, 22 Nov 2008, *Felger 08-193* (DES). †M. cf. grahamii, Tinajas Altas, spines, seeds, 1230 to 18,700 ybp (11 samples).

Mammillaria tetrancistra Engelmann
Corkseed fishhook cactus; *cabeza de viejo*. Figure 26 D–G.

Stems single (unbranched) or with 1 to several branches, areal part of stems globose to cylindroid, and often 5–10 × 3.5–6 cm; underground portion of stem usually thickened, flabby, root-like, often 5–8 cm long; upper part of roots also often thickened. Spines dark or light colored depending largely on substrate color (see *Ferocactus cylindraceus* and *Mammillaria grahamii*); central spines hooked, 1–3 (4) per areole. Flowers 2.5–3.5 cm wide, pink, spring and summer, and not arranged in a ring (as in *M. grahamii*). Outermost tepals with relatively long-fringed margins (use hand lens; figure 26-E). Inner tepals pink-magenta, often with paler-colored margins. Stigma yellow or yellow-green. Fruits succulent, bright red and longer than wide. Seeds (not including strophiole) 1.6–2.4 mm at widest point, the surface rugose-roughened over a reticulate cellular pattern and not pitted; basal 1/3 of seed covered with a light-colored, corky aril-like cup (the *strophiole,* a specialized outgrowth or proliferation of hilum tissue), the strophiole pale colored and spongy when fresh, drying brown and corky and remaining firmly attached to the seed. Although the fleshy part of the fruit is edible, the seed cork will make you spit it out—an easy way to identify this species.

Rocky soils, hills and mountains, and sometimes adjacent middle to upper bajadas, from the Tinajas Altas Mountains across Cabeza Prieta, and lower elevations in Organ Pipe. Often growing intermixed with *M. grahamii.*

Western Arizona, southeastern California, southern Nevada, southwestern Utah, northwestern Sonora, and northeastern Baja California.

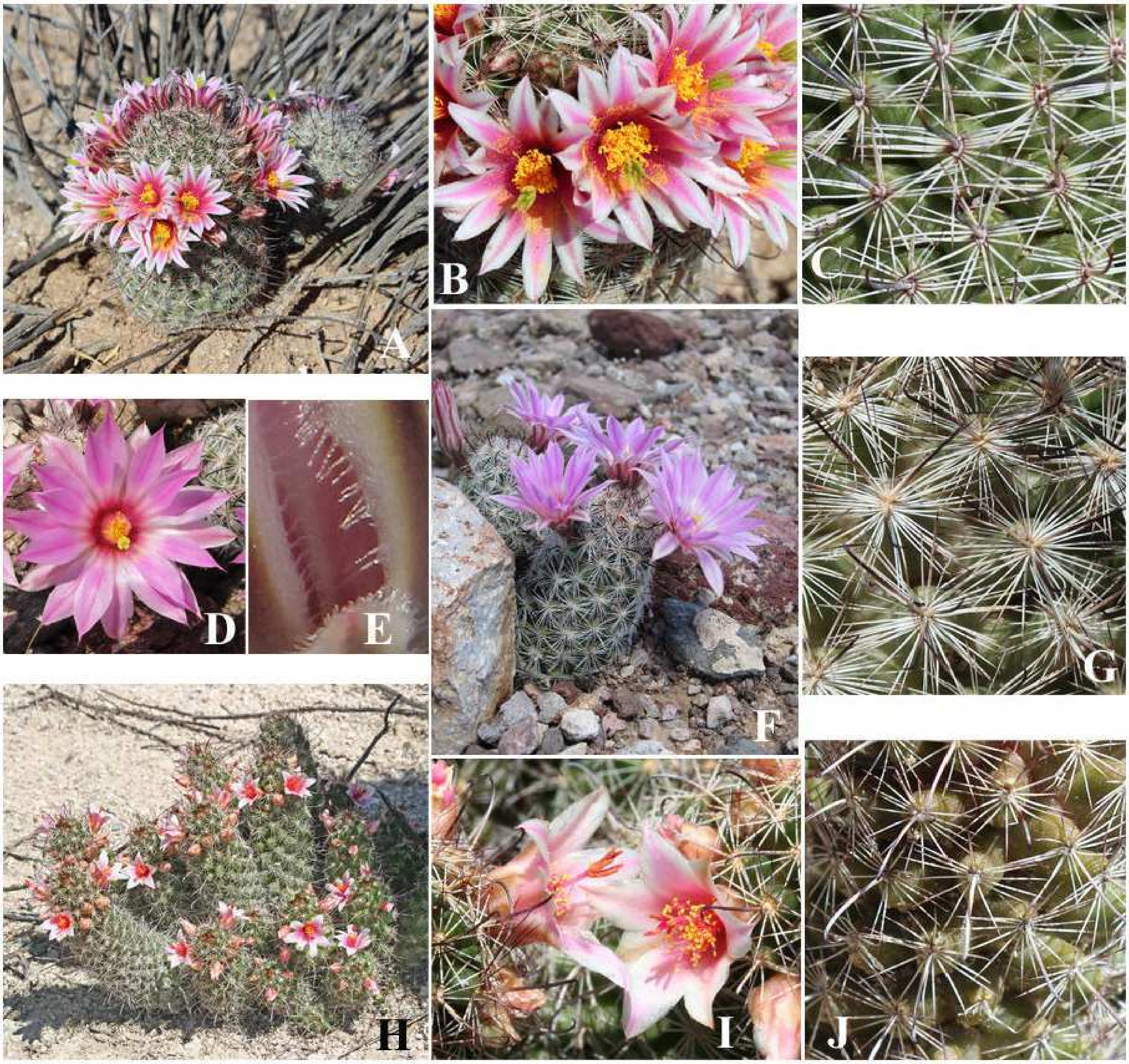

Figure 26. *Mammillaria grahamii*: (A & B) SW of Hwy 85 & Armenta Ranch Road, Organ Pipe, 30 Jul 2013; (C) Ajo, 6 Sep 2013. *Mammillaria tetrancistra*: (D & E) flower and tepal margin, El Huerfano, Sonora, 5 Sep 2013; (F & G) N of Dos Lomitas, Sonoyta Valley, Organ Pipe, 23 Aug 2012. *Mammillaria thornberi*: (H & I) W of Quitobaquito, 13 Sep 2006; (J) near El Huerfano, Sonora, 26 Aug 2013.

The plants are deceptively similar to *M. grahamii* when not in flower although they are not closely related within the genus. Apart from the distinctive seeds and flowers, *M. tetrancistra* may be identified by its relatively smooth, soft, extensive, and deeply buried stem-base (often wedged between rocks); surprisingly soft-skinned and flaccid stems and tubercles (not firm like those of *M. grahamii*); mucilaginous pith and cortex (tangible even on the smallest cut surfaces, such as tubercle sections); radial and subcentral spines that do not radiate as neatly and regularly as those of *M. grahamii*, giving the plant a relatively shaggy appearance or a "salt-and-pepper" color-pattern rather than a "well-groomed" appearance; and narrower and more numerous tepals, the outer tepals with relatively large fringes. The seeds of *M. tetrancistra*, with their corky base, are unlike those of any other cactus. It is the most arid-inhabiting of all mammillarias.

OP: 0.5 mi N of Mexican Border, 3 mi E of Lukeville, 6 Jan 1962, *Steenbergh 1-662-1* (ORPI). Growler Mine, Bates Mts, 13 Sep 2013, *Rutman*, photos.

CP: Near Tule Mts, 4 mi E of Tule Well, 29 Feb 1976, *McManus 688*. T15S, R12W, S18, lava flow, 7 Apr 1979, *Lehto L23574* (ASU). Childs Mt, 2240 ft, 9 Apr 1993, *Felger 93-303*. Growler Mountains, S of Charlie Bell Pass, 9 Apr 1993, *Felger* (observation).

TA: Granite hills at SW side of Tinajas Altas Mts, 10 Jan 2002, *Felger 02-6*. Camino del Diablo SSE of Raven Butte, 20 Feb 2005, *Felger* (observation).

Mammillaria thornberi Orcutt
[*M. fasciculata* of authors, not Engelmann]
Thornber fishhook cactus; *cabeza de viejo*; ban mauppa. Figure 26 H–J.

Stems often (2) 3–3.5 cm diameter, more than twice as long as wide, usually somewhat flaccid, branching from the base and along the stem to eventually form spreading, many-stemmed plants, these sometimes breaking apart, the pieces forming adventitious roots, or the plants occasionally with only a few branches. Hooked central spines 1 per areole. Inner tepals white or pale pink with a bright rose-pink midstripe. (The inner tepals are broader than those of the two other mammillarias in the region). Filaments rose-pink; anthers yellow. Stigma magenta. Seeds 0.9 mm diameter, similar to those of *M. grahamii*. Flowering July and August.

Locally common along the southern margin of Organ Pipe and also in the northwestern part of the Monument. Sandy to gravelly soils of lower bajadas and desert flats, usually under small shrubs, especially *Ambrosia deltoidea*, *A. dumosa*, *Atriplex linearis, A. polycarpa* and sometimes among fallen joints of *Cylindropuntia fulgida*, and rarely under *Suaeda nigra*. Highest density is in saltbush vegetation on Holocene-aged surfaces. Often growing intermixed with *M. grahamii*.

Southwestern Arizona and northwestern Sonora southward to sandy plains southwest of Caborca.

Mammillaria thornberi is closely related to, but obviously distinct from, *M. yaquensis* R.T. Craig, which occurs on fine-textured, alluvial soils of the coastal plains of Sonora from near Empalme and Las Guásimas (southeast of Guaymas) southward to northwestern Sinaloa. The two species are disjunct by several hundred kilometers. *Mammillaria yaquensis* differs in part by its markedly more delicate and slender stems and more profusely branching habit, the branches often arise well above the lower part of the stem, and smaller and more readily detaching branches. There is no indication of plants with intermediate features.

OP: Quitobaquito, 28 Nov 1939, *Harbison 26183* (SD). 10 mi E of Hwy 85 on Mexican Boundary, 26 Jan 1962, *Steenbergh 1-2662-1* (ORPI). Hocker Well, 3 Dec 1990, *Felger 90-575*. 0.5 mi W of Growler Wash on Bates Well Rd, loamy flat, under *Larrea*, *Rutman 23 Aug 2001* (ORPI).

†**Mammillaria** sp.
TA: †Butler Mts, hooked spines, 740 & 3820 ybp.

Opuntia – Prickly-pear; *nopal*

Stem segments, or pads (cladodes), laterally compressed. Areoles bearing glochids and with or without spines. Areoles of young developing pads and flowers (fruits) bearing extrafloral nectaries and a small, green, succulent, conical, and soon-deciduous leaf. Flowers relatively large, diurnal, with sensitive stamens (filaments closing inward when touched). Fruits fleshy or dry. "Seeds" relatively large, the actual seed covered with a white to light tan bony aril-like structure (see *Cylindropuntia*).

The genus includes about 150 species, native from Canada to South America.

1. Pads 9–12.5 cm long, generally bluish to purplish, minutely hairy (use 10× lens); areoles with glochids but spines lacking; inner tepals rose-pink. .... **Opuntia basilaris**
1. Pads usually 15 cm long or more, glabrous, green or sometimes reddish purple; areoles with glochids, and at least some areoles with spines; inner tepals yellow to pale orange (tepal bases reddish in *O. phaeacantha*).
    2. Plants erect, often with a short but well-developed trunk; pads more or less orbicular; spines yellowish, becoming blackish with age, mostly pointing downward. .... **Opuntia chlorotica**
    2. Plants often sprawling-spreading, trunk not well developed; pads obovate to elliptic; spines mostly white with brownish bases or if yellow then relatively robust and the largest one porrect and/or spreading (pointing in different directions).
        3. Flowers uniformly yellow when first open, becoming pale orange with age but of a single color; fruits very juicy, the pulp and skin rich red-purple..................... **Opuntia engelmannii**
        3. Flowers yellow with a conspicuous reddish center; fruits only moderately juicy, the skin pinkish to reddish, the pulp whitish or greenish, not bright purple........ **Opuntia phaeacantha**

Opuntia basilaris Engelmann & J.M. Bigelow var. **basilaris**
Beavertail cactus. Figure 27.

Dwarf prickly-pears, often 25–50 cm wide, forming a very thick, short caudex giving rise directly to thick, stubby pads that sometimes curl inward. Individual stems of 1 or rarely 2 pads (cladodes). Pads 8–14 × 4–10 cm (reaching 18 cm long in cultivation), the surfaces minutely and densely puberulent (use 10× lens), pale bluish (the color does not rub off), somewhat pale purplish during cooler, drier months. Areoles bearing dense tufts of glochids, which are barbed, but no spines. Young areoles on developing pads have transparent tubular hairs and minute, cone-shaped red leaves, which are pubescent with minute, short, thick hairs; leaves soon deciduous. (Marc Baker observed small black ants apparently feeding on surface compounds of the tubular hairs of the areole and of the small hairs on the leaves of a plant from the type locality of *O. basilaris*. A test with Benedict's Reagent, however, did not detect simple sugars). Flowers 7–7.5 cm wide, showy, opening for 1 or 2 days; outer tepals thick and fleshy, greenish brown, the inner tepals bright rose pink, 4–4.5 cm long, the larger tepals 2.5–3 cm wide. Filaments red; anthers pale yellow: the showy stamens with red filaments and yellow anthers are noteworthy. Style pale rose pink, darker on the second day; stigmas pale yellow, opening on the second day. Fruits dry at maturity. "Seeds" 7–9 mm wide, puffy, looking like compressed garbanzo beans. Flowering in early April, the fruits ripening in late May; $2n = 22, 33$ (M. Baker, unpublished data).

Arid, western margin of the flora area: southwestern corner of Cabeza Prieta and the Tinajas Altas Mountains. On nearly barren desert pavements, canyons and rocky slopes, and also granitic mountains in adjacent Sonora west of the Pinacate lava (Felger & Zimmerman 2000). No other prickly-pear extends into such hyperarid regions. This small prickly-pear ranges from the pediment base to nearly the summit in the Tinajas Altas Mountains; at higher elevations it occurs in localized soil pockets. Its history in the Tinajas Altas region extends to more than 37,000 years.

Many pads have a dead, dried area below the old flower or fruit—the pad tips desiccate. In drought conditions the pads shrivel and wrinkle, and some or even most or sometimes all of the pads drop off in severe drought like deciduous leaves. Thus, in the most severe drought conditions the thick, succulent caudex functions like a thick, tuberous root. The pads are relatively dwarfed in comparison with those of the same variety of beavertail cactus from other regions, but in cultivation (in Tucson) the pads of plants from the flora area can become substantially larger than ones seen in the wild.

Western Arizona, northwestern Sonora, southern California, southern Nevada, southwestern Utah, and northern Baja California. Several varieties are recognized; variety *basilaris* nearly encompasses the distribution of the entire species. In 2014 Rutman observed beavertail plants volunteering in some Ajo neighborhoods, presumably from seeds dispersed by birds from cultivated plants.

Richard writes: "I remember my first cactus collection. My family had gone to Palm Springs, California, for a vacation. I was five or six years old and fascinated by a beavertail cactus and put a pad in my pocket. Much later I learned that the highly irritating glochids can be removed with adhesive tape or shaving the afflicted surface (the glochids eventually dissolve)." Bean and Saubel (1972: 95) report that the Cahuillas in California ate the fresh fruits and that the flower buds were pit-baked or sometimes dried and stored, the pads boiled as a vegetable, and the "seeds ground into an edible mush." This is one of few references to *Opuntia* "seeds" being eaten. The fruits hardly seem worth eating "fresh" since they are dry at maturity, or maybe they were harvested just before becoming dry?

CP: E edge of Lechuguilla Desert (Simmons 1965, 1966). Bajada of Tordillo Butte, 4 mi on Camino del Diablo E of the W border of the Refuge, basalt-sand flat outflow from Tordillo Butte to the NE, 16 Jun 1992, *Felger 92-621*.

TA: Observations, *Felger*: Borrego Canyon, 3 Feb 1990; Tinajas Altas, 29 Nov 2001. Tinajas Altas Pass, 32.31444°N, 114.08556°W, 329 m, rocky granitic slope and derived gruss, 2 Mar 2014, *Susan Davis Carnahan*, 2 photos (MABA in SEINet). Variety unknown: †Tinajas Altas, seeds, 1230 to 11,040 (8 samples), & >37,000 ybp.

Opuntia chlorotica Engelmann & J.M. Bigelow
Pancake prickly-pear; *nopal rastrero*. Figure 28.

Shrub-sized prickly-pears, often 1–1.6 m tall, developing a short, stout trunk. Pads (10) 13–23 × (10) 13–25 cm, erect, oval, obovate, or nearly round in outline, moderately glaucous, not becoming reddish or purplish. Areoles all bearing spines, or a few lowermost areoles without spines. Spines straw colored, mostly pointing downward; persisting on older pads and trunk and becoming grayish or blackish, those of lower areoles often long and shaggy. Flowers large, inner tepals yellow with a faint red midstripe even when freshly open; stigmas green. Fruits fleshy, glaucous, rose pink. Flowering in April. $2n = 22$.

Middle to higher elevations in mountains, especially in the northern and eastern part of the flora area; absent from lowland flats. Rare, single plants, however, occur where it is not expected, e.g., Sue Rutman found one plant in the 1990s at the base of the Pozo Nuevo Hills and another one in 2013 in Acuña Valley.

Unlike most other cacti in the region, this species seems to have expanded its range in the wetter rainfall climates of the Wisconsin glacial environments, a time of greater winter rainfall and drastically reduced summer rains. It is documented in Organ Pipe for 32,000 years, and more than

11,000 years in Tinajas Altas where it no longer occurs.

Arizona, northern Sonora, Baja California, northwestern Chihuahua, southeastern California, southern Nevada, New Mexico, and southwestern Utah. In the Sonoran Desert region this prickly-pear is characteristic of the upper edge of the desert, desert-oak woodland ecotone, and often occurs in oak woodland.

Figure 27. *Opuntia basilaris*. (A) Tinajas Altas, 28 Apr 2010, photo by Jim Malusa. Kofa Mts: (B) flower, near Palm Canyon, 5 Apr 2014; (C) fruit, road between Palm Canyon and Kofa Queen Canyon, 6 Apr 2014. (D) Young cladode, volunteer plant in Ajo yard, 3 Apr 2014. (E) Desiccating cladode, Horse Tank, Castle Dome Mts, 6 Apr 2014.

The fruits, comparatively smaller and drier than those of *O. engelmannii*, were probably seldom eaten if *O. engelmannii* fruits were available. Gifford (1936), however, reports that the Yavapais ate the fruits. Castetter and Underhill (1935: 16) report "an upright species of prickly pear . . . is utilized by washing the large waxy flowers to remove their sticky secretion then frying them in grease, formerly deer fat, now lard." That prickly-pear probably was *O. chlorotica*, which indeed has an upright habit.

Figure 28. *Opuntia chlorotica*. (A) N of Pinkley Peak, Puerto Blanco Mts, 31 Oct 2003. (B) Estes Canyon, 25 Apr 2013. (C) Alamo Canyon, 12 Jan 2014.

OP: Ajo Mts, 3000 ft, *Nichol 28 Mar 1939* (ORPI). Puerto Blanco and Santa Rosa Mts (Bowers 1980). Observations: 1.9 mi by road N of Bates Well, N boundary of Organ Pipe, 30 Jan 1992, *Felger*; Trail from The Cones to Mount Ajo, 4090 ft, 10 Apr 2005, *Felger*; Acuña Valley in lower foothills of western Puerto Blanco Mts, one plant seen, 30 Jan 2013, *Rutman*. †Alamo Canyon, seeds, 1150 to 32,000 ybp (7 samples). †Montezuma's Head, seeds, 13,500 to 21,840 ybp (4 samples). †Puerto Blanco Mts, on ridge, seeds, 8790 to 14,120 ybp (5 samples.

CP: 7 mi E of Papago Well, *Harbison 16 Mar 1937* (SD). Observations, *Felger*: Sheep Mt, N side, mid-elevation to summit, 31 Jan 1992; Hills at E boundary of Refuge along Charlie Bell Rd, 12 & 13 Jun 1992; Agua Dulce Pass, 12 & 13 Jun 1992.

TA: †Tinajas Altas, seed, 11,040 ybp.

Opuntia engelmannii Salm-Dyck ex Engelmann
Prickly-pear; *nopal*; naw, 'i:bhai

Medium-sized to large sprawling, prickly-pears, usually trunkless. Pads remaining green all year. Flowers uniformly bright yellow, becoming pale orange (apricot color) as they age, the flowers generally opening a second day. Flowering (March) April and early May. Fruit skin and pulp red-purple, the pulp sweet, juicy, and edible; fruits mostly ripen in July.

Northern Mexico and southwestern United States. Five varieties are recognized (Pinkava 2003d), with var. *engelmannii* being the most widespread.

Prickly-pears were an important food resource for the Hia Ced and other O'odham people. The young pads were harvested in late spring and summer, the spines and glochids removed, and the pads cooked as a vegetable, and the fruits eaten fresh or cooked and made into jam (e.g., Betty Melvin in Zepeda 1985; Castetter & Underhill 1935). "We would squeeze the juice from the ... fruit. ... It is better tasting than any drink. ... Early in the morning when [it] is a little cool, we would gather them. A whole box full. I would get them and squeeze the juice out ... it is so good" (Betty Melvin in Zepeda 1985: 82, 83).

1. Pads markedly elongated, more than twice as long as wide ....**Opuntia engelmannii** var. **linguiformis**
1. Pads not markedly elongated, to about 1.5 times longer than wide.

    2. Branches often sprawling or spreading; spine color various, often ashy gray or sometimes reddish brown at the base and lighter colored (white coated) near the tip; larger spines often 3–5 per areole, mostly straight, largest spines 3–6.2 cm long...**Opuntia engelmannii** var. **engelmannii**
    2. Branches commonly held well above the ground, or the plants sometimes spreading; spines bright yellow (not white coated), the larger spines often 1 per areole (seldom more than 3), often curved, largest spines 4.5–7.7 cm long. .... **Opuntia engelmannii** var. **flavispina**

Opuntia engelmannii var. **engelmannii**
[*O. discata* Griffiths. *O. phaeacantha* Engelmann var. *discata* (Griffiths) L.D. Benson & Walkington]
Desert-prickly pear. Figure 29.

Robust prickly-pears, trunkless or nearly so, usually spreading or sprawling, sometimes reaching 1–1.8 m in height, the larger colonies sometimes reaching 3–4+ m across. Pads obovate to elliptic, (18) 20–33 × 16–23 cm, and about 1 cm thick, remaining green all year. Spines often 3–5 per areole, the larger ones 3–6.5 (7.7) cm long, straight or curved, yellowish to red-brown, often bleaching white with age; spine-bearing areoles often extending to the base of the pad. Flowers often 7.5–9.5 cm wide; inner tepals uniformly bright yellow, becoming yellow-orange (apricot color) as the flowers age (usually the second day); filaments and anthers pale yellow, the style white, the stigma green; flowering in spring, mostly April and May (at the same times as *O. phaeacantha*). Fruits 5.5–7.5 × 3.5–4 cm, reddish purple including the pulp, the pulp juicy and sweet, ripening in late July and August. $2n = 66$ (Baker et al. 2009).

Widely scattered in Organ Pipe and the eastern part of Cabeza Prieta including the Agua Dulce and Growler Mountains; above 1650 feet on desert flats, bajadas, pediments, hills and mountains. Above 3400 feet in the Ajo Mountains this species commonly occurs with *Juniperus arizonicus*, *Simmondsia chinensis*, and *Vauquelinia californica*. "Fruits and pads relished by rodents and other mammals including javelinas" (Simmons 1966: 102).

Texas to southwestern Utah and southern California and southward to the adjacent border states in Mexico.

OP: W side of Ajo Mts, *Nichol Mar 1939* (3 sheets, ARIZ 64930, 83680, & 135545). Alamo Canyon, *Nichol 1 May 1939* (ORPI, POM/RSA). 10 mi on road east from Headquarters, 2500 ft, 14 Nov 1955, *Benson 15615* (3 sheets each accessioned as POM/RSA 284081). S end Sierra Santa Rosa, 22 May 1989, *Baker 7761* (ORPI). Quitobaquito, old fields, 11 Aug 1990, *Felger 90-430*. Observations, *Felger*: 0.2 km W of Hwy 85 at N boundary of Monument, 23 May 1991; Hocker Well, 3 Dec 1990.

CP: Bluebird Mine, 1800 ft (Simmons 1966). Observations, *Felger*: Agua Dulce Pass, 12 & 13 Jun

1992; S of Charlie Bell Road on road to Lower Well; Childs Mt, 2400 ft, 18 Aug 1992; *Malusa:* Near Temporal Pass, Growler Mts, UTM (Zone 12N), 3573000 E, 309700 N (NAD 1927), 1800 feet, 19 Feb 2000.

Opuntia engelmannii var. **flavispina** (L.D. Benson) B.D. Parfitt & Pinkava
[*O. phaeacantha* var. *flavispina* L.D. Benson]
Yellow-spine prickly-pear. Figure 30.

This prickly-pear is distinguished from var. *engelmannii* by having the branches held well above the ground and the plants generally with a more erect habitat and not sprawling, with relatively fewer, often longer spines (4.5–7.7 cm long), often curved and bright yellow (not white coated), often 1 or 2 per areole (seldom more than 3 large spines per areole), the spines arching downward, and often larger fruits. Flowers similar in size and color to those of variety *engelmannii*. Records from the 1980s and 1990s document plants of this prickly-pear to 1.5 m tall, but following the severe drought of the 2000s, Sue Rutman has not seen them this large, at least not in Organ Pipe.

Figure 29. *Opuntia engelmannii* var. *engelmannii*. Mouth of Alamo Canyon, Ajo Mts: (A) 18 Nov 2003; (C) 25 Apr 2013; (D) 21 May 2006. (B) Lukeville, 5 Sep 2013. (E) Near Armenta Ranch Road E of Hwy 85, 31 Jul 2013.

This rather distinctive variety occurs in relatively small populations in the Ajo Mountains, at Quitobaquito and scattered westward along the northern edge of the Río Sonoyta in Sonora to the vicinity of Corner Well, and near prehistoric sites such as Agua Dulce Pass. Sue Rutman found one plant in 2011 about one mile north of Dos Lomitas near a prehistoric trail from Mexico to Sweetwater Pass.

The population at Quitobaquito in the 1990s was small, with about one dozen adult plants and seemed to be increasing due to discontinuation of cattle grazing. The plants were vigorous and juvenile plants were present (Felger et al. 1992). However, in the decade preceding 2014, plants at

Figure 30. *Opuntia engelmannii* var. *flavispina*. International boundary W of Quitobaquito: (A) 5 Sep 2013; (B) 13 Sep 2006; (C) 26 Aug 2013; (D) 22 Apr 2008.

Quitobaquito and westward were barely surviving due to drought. This prickly-pear occurs at former O'odham village and farming areas and may represent introduction and/or selections by the local people (Felger et al. 1992). Variety *flavispina* and var. *engelmannii* plants occur intermixed without apparent intermediates.

Variety *flavispina* is known only from southern Arizona in Maricopa, Pima, and Yavapai Counties and Sonora near the flora area (near the northern edge of the Río Sonoyta).

OP: Alamo Canyon, 2300 ft, *Nichol 27 Apr 1939* (isotype: ORPI). Quitobaquito Springs, 1100 ft, shrub to 1.5 m tall, 2 m broad, fruit purple-red, 17 Aug 1988, *Baker 7625* (ASU, ORPI). Quitobaquito, old fields, 11 Aug 1990, *Felger 90-431*. Hocker Well, 3 Dec 1990, *Felger* (observation). Quitobaquito Springs, 300 m N of Mexico, in the vicinity of the spring, 1080 ft, shrub 1m tall, as broad, with leaning trunk, main spine pale yellow-brown, to 7 cm long, others twisting and curving, several plants in area, mostly smaller, *n* = 33, 19 Mar 1992, *Baker 8788* (ASU; cited in Haseltonia 6: 35, 1999).

CP: N slope of Agua Dulce Mts, along road 0.3 mi below Agua Dulce Pass, 1550 ft, granitic rock, rare, 1.5 m tall, the branches held well above the ground, dry [old] fruits red-purple, 14 Sep 1992, *Felger 92-737* (ASU, DES).

****Opuntia engelmannii** var. **linguiformis** (Griffiths) B.D. Parfitt & Pinkava
[*O. linguiformis* Griffiths]
Cow-tongue prickly-pear. Figure 31.

Large, sprawling plants, propagating vegetatively, and distinguished by markedly elongated stem segments of indeterminate growth. Flowers large and yellow; the plants apparently sterile.

Cultivated at Lukeville and Sonoyta and sometimes becoming weedy. Large pieces of this unattractive cactus dumped in the desert as trash are the sources of the plants east and west of Lukeville, less than 200 m north of the international border. The plants seem to persist but apparently are not spreading.

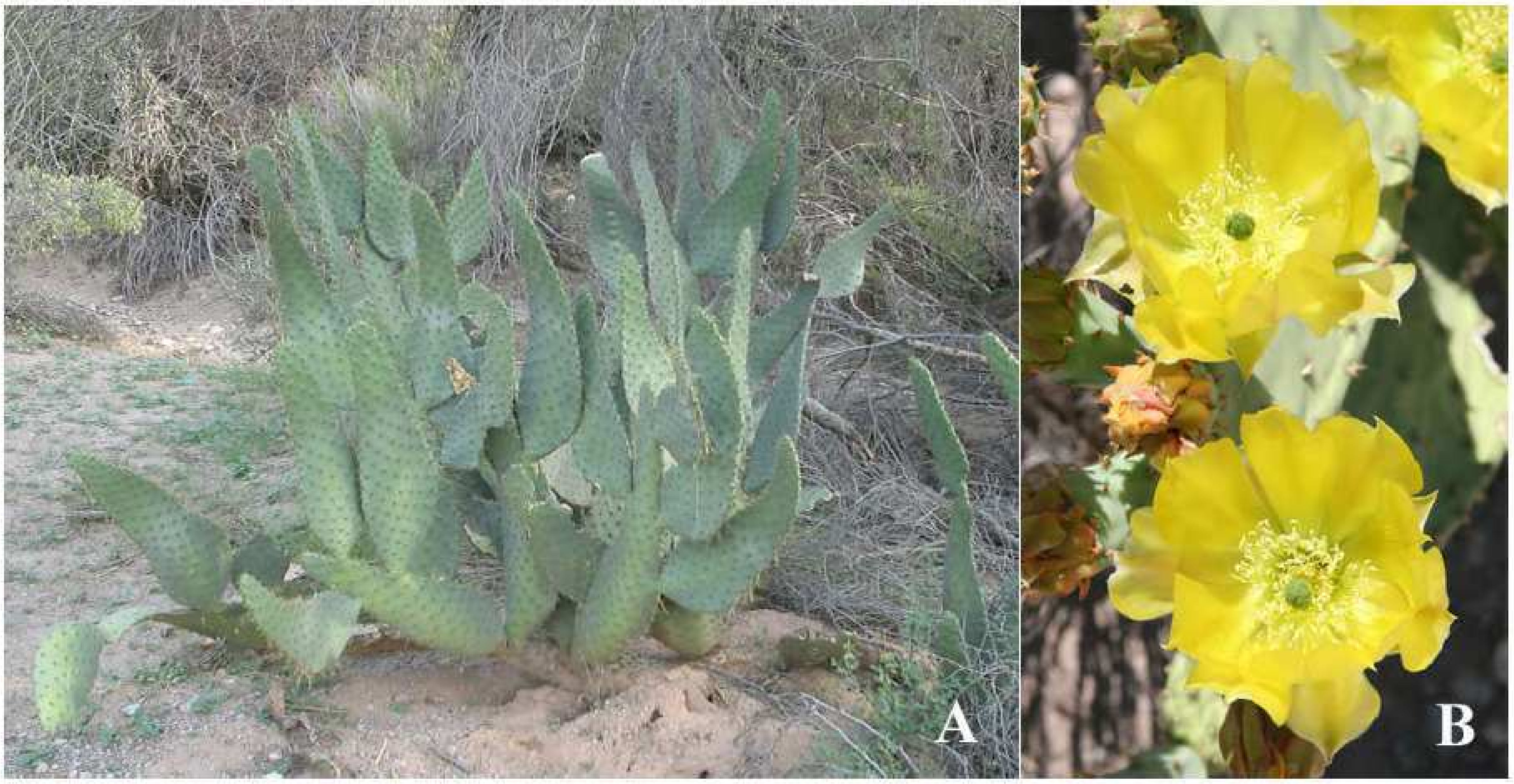

Figure 31. *Opuntia engelmannii* var. *linguiformis*. Lukeville: (A) 30 Oct 2003; (B) 21 May 2006.

This prickly-pear is widely cultivated and is sometimes feral in southern Arizona (perhaps resulting from trash-dumped plants). Also in southern New Mexico, southern Texas, and northern Mexico. No native populations are known for certain (Anderson 2001; Parfitt & Pinkava 1988; Pinkava 2003d). A cultivated individual from east of Tucson was a pentaploid, 2*n* = 55 (Baker et al. 2009); all other counts in the literature for this taxon have been hexaploid.

OP: Observations, 3 Nov 2003, *Rutman*: Within 1 mi E of Lukeville and less than ¼ mi N of the international boundary, between Lukeville and Gachado Line Camp, few dozen plants, growing from dumped plants; About ½ mi N of Lukeville on Hwy 85, 100 ft W of highway in a grove of *Prosopis* & *Atriplex*; Less than a few hundred feet N of the international boundary, dissected hills between Lukeville and Dowling Ranch, several plants.

†Opuntia engelmannii and/or **O. phaeacantha**

We are not able to distinguish these two prickly-pears with fossil seeds.

OP: †Alamo Canyon, seeds, 1150 to 32,000 ybp (6 samples). Puerto Blanco Mts, on ridge, seeds, 980 to 7970 ybp (5 samples; *O. engelmannii* var. *engelmannii* presently occurs in washes below the midden site, but not on the rocks at the midden site).

Opuntia engelmannii and *O. phaeacantha* may hybridize and the resulting variation can be perplexing. For example, *O. phaeacantha* plants known to have red-centered flowers can also have fruits with red-colored rind, the pulp being whitish or even reddish. Sometimes the hexaploid *O. engelmannii/phaeacantha* complex can be seen as a super species or species complex, with no hard and fast rules, only trends, and the trends can be localized. Some cactus enthusiasts and botanists have recognized dozens of species within the complex, many of which are probably apomictic clones or microspecies. In the flora area as well as elsewhere, *O. engelmannii* and *O. phaeacantha* often occur together. The morphology at both ends of the gamut is so different that people have a difficult time not wanting to keep them as separate species. Perhaps DNA studies will eventually help clarify the problem. For example, David Griffiths (1867–1935) named more than a dozen species at both ends of the gamut as well as morphological intermediates in many localities based on minor differences. Some people have picked up these names and claim they can identify them and perhaps they can but the question is: Are they worthy of taxonomic recognition and, if so, is there any way to make a key so that you or I or anybody else can identify them? The problem may be likened to that of the dog, where there are a myriad of forms but all belonging to the same species.

Opuntia phaeacantha Engelmann
Brown-spine prickly-pear; *nopal*. Figure 32.

Low, spreading prickly-pears, sometimes to 0.5 m tall, generally much wider than tall, often forming trailing stems of several or more pads. Pads becoming moderately reddish purple in winter and spring. Areoles often bearing long, stout, and sometimes darkish and spreading spines. Young central spines usually reddish brown, becoming ashy gray with age. Central spines usually lacking or much reduced on the lower (proximal) part of the pads. Flowers, especially when first opening, yellow with a reddish-orange center; flowering in April and May. Fruits ripening in July.

Eastern part of Organ Pipe; upper and middle bajadas and less common on lower slopes of the Ajo and Diablo Mountains. Often growing with *O. engelmannii*. Also common northward from Organ Pipe in some areas of the Sauceda, Sikort Chuapo, and Sand Tank Mountains.

A highly polymorphic species; California to Kansas and Texas and northern Mexico.

The fruits of this species are generally smaller, less juicy, and much less desirable for eating than *O. engelmannii* fruits (Felger 2007; Pinkava 2003c). Castetter and Underhill (1935: 22) report that the O'Odham (Papago) "distinguish two kinds of edible prickly pears (*Opuntia* sp.), one of which produces chills and nausea in susceptible people." This statement likely refers to *O. phaeacantha*, while the other kind is probably *O. engelmannii*.

Although the differences between *O. engelmannii* and *O. phaeacantha* are subtle and perplexing, they usually can be distinguished in the flora area using a suite of key features. *Opuntia phaeacantha* tends to form shorter and more sprawling plants, the stems often trailing, and there are differences in the pattern of the glochids in the areoles (Pinkava 2003c, d). Sue Rutman finds two main field characters when the plants are not blooming: First, the central spines are absent or reduced on the lower third of the cladode in *O. phaeacantha*, while central spines extend to the base of the pad in *O. engelmannii*. Second, the shape of the *O. phaeacantha* pad is more elongated than the rounder (circular) shape of *O. engelmannii*. The Organ Pipe and Sauceda Mountain populations of *O. phaeacantha* generally have long and more obviously spreading and rather dark spines, and in winter

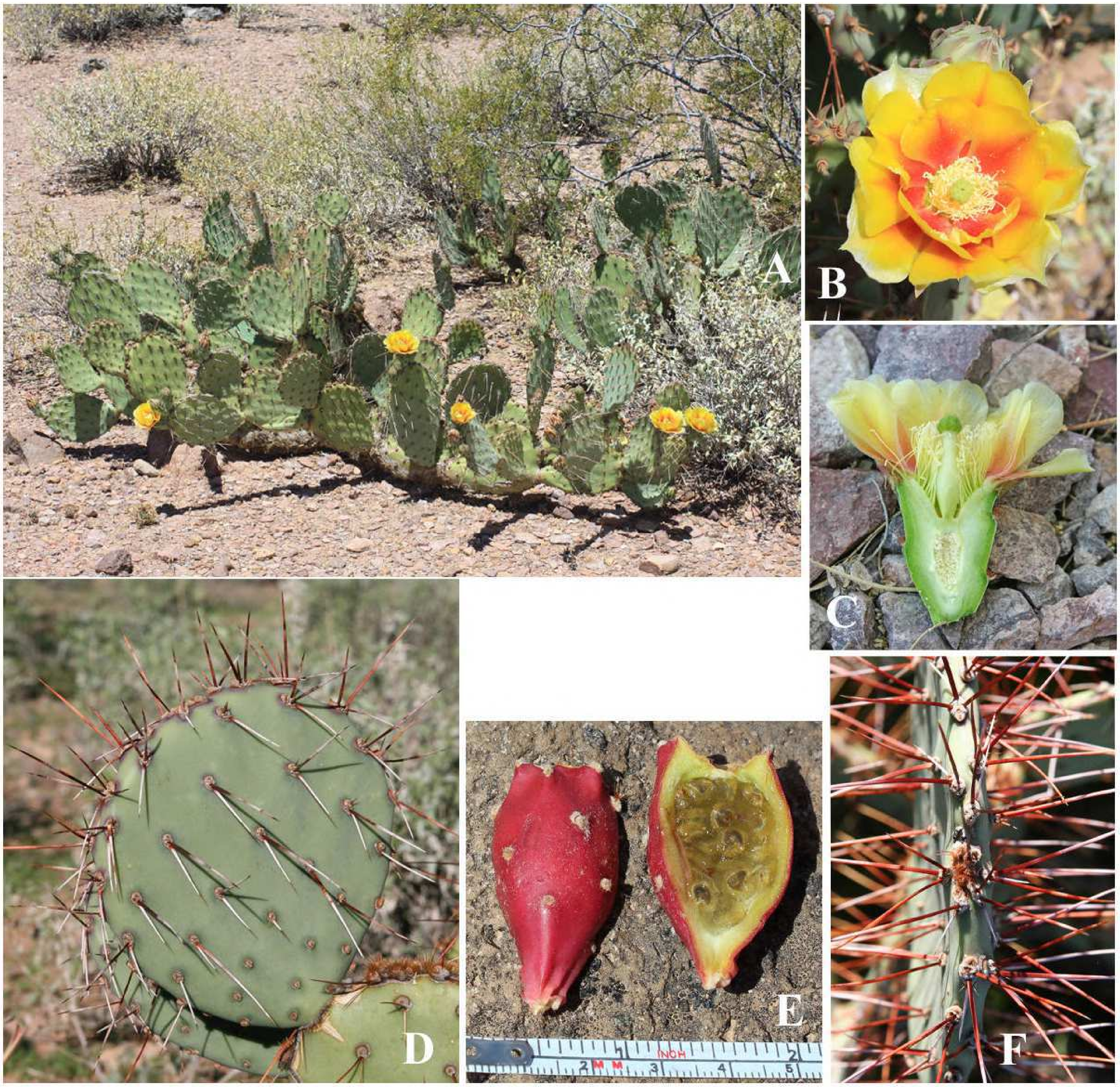

Figure 32. *Opuntia phaeacantha*. Mouth of Alamo Canyon, Ajo Mts: (A & B) 25 Apr 2013; (C) 21 May 2006; (D) 27 Jan 2009, (F) 27 Jan 2009. (E) Near Ryan Wash, Sauceda Mts, 4 Aug 2013.

and the spring dry season the pads tend to become purplish or brownish at least in part. The bicolored flowers (yellow with a reddish center) provide a clear-cut diagnostic distinction, and are evident as soon as a flower opens. The flowers (tepals) of both species become yellow-orange or peach-colored as they age, even during the afternoon of first day if the weather is hot, and probably always on their second day, which can obliterate the ability to distinguish these two prickly-pears. Flowers of *O. phaeacantha* can be smaller than those of *O. engelmannii.* The fruits of *O. phaeacantha* tend to be narrow and cylindroid, typically the "skin" is dull pinkish (pinkish orange in the extreme form) or brick red, and the pulp is typically lighter in color, not purple-staining, and not especially juicy (but "over-ripe" fruits can become juicier and redder), and the pulp not sweet and not very good to eat. In contrast the fruits of *O. engelmannii* are plumper, generally larger, and more egg-shaped, and the "skin" and pulp brilliant, dark purple, beet red, or burgundy, and the pulp decidedly sweet and juicy.

OP: Boulder Canyon, 3500 ft, 24 May 1962, *Steenbergh S-2482-5* (POM/RSA). 0.5 mi N of Alamo Canyon campground on Alamo Canyon road, with *O. engelmannii*, *Rutman 26 Apr 2002.* Gunsight Hills, 14 Mar 2003, *Rutman 2003-535* (ARIZ, ORPI). Flowers from part of same plant as *Rutman 26 Apr 2002*, grown in Tucson, *Felger 14 May 2005.*

****Opuntia santa-rita** (Griffiths & Hare) Rose
Purple prickly-pear

Upright-growing prickly-pear, often reaching about 1 m tall. The pads become purplish during cool and dry seasons. An attractive plant, often cultivated.

A specimen labeled Quitobaquito is likely to be from a cultivated plant, and seems to be the source of Benson's (1982) mapping of this species in Organ Pipe (Felger et al. 1992).

OP: Quitobaquito, *Nichol 27 Apr 1939* (ORPI).

Peniocereus – Night-blooming cereus
Slender-stemmed cacti with tuberous roots. Stems appearing cryptic, mimicking shrub and tree branches. Areoles with relatively small spines, the central and radial spines similar; areole glands none. Oldest stems at base of plants becoming woody and without fleshy tissue. Flowers (those in the flora area) relatively large, white, nocturnal, and fragrant; adapted for pollination by hawk moths (Sphingidae). Fruits red and juicy. This genus as a natural (monophyletic) group includes 7 species in Mexico (Arias et al. 2005), 4 of which occur in the Sonoran Desert, and 2 of them range into southwestern USA.

Only a relatively few species in the entire cactus family have truly tuberous roots, which seems rather surprising, and they all have rather small stems (Mauseth 2014; Stone-Palmquist & Mauseth 2002). Seven Sonoran Desert cacti have conspicuous tuberous roots. Six occur in Sonora: *Echinocereus leucanthus* N.P. Taylor, *Grusonia marenae* (W.E. Parsons) E.F. Anderson, *G. reflexispina* (Wiggins & Rollins) E.F. Anderson, *Peniocereus greggii, P. marianus* (Gentry) Sánchez-Mejorada, and *P. striatus.* Two occur in the Baja California Peninsula: *Peniocereus johnstonii* Britton & Rose and *P. striatus.* The four *Peniocereus* grow on fine textured lowland soils as well rocky habitats and sometimes even in bedrock. The *Echinocereus* and two *Grusonia* only occur on lowland, sandy or fine-textured soils.

1. Stems reaching 20 mm diameter, with 4 or 5 (rarely 6) ribs. .... **Peniocereus greggii**
1. Stems 4.5–8 mm diameter, with 6–9 flat-topped ribs separated by narrow furrows or grooves .... **Peniocereus striatus**

Peniocereus greggii (Engelmann) Britton & Rose var. **transmontanus** (Engelmann) Backeberg [*Cereus greggii* Engelmann var. *transmontanus* Engelmann]
Desert night-blooming cereus; *reina de la noche, sarramatraca*, ho'ok wa', ho'isa (Betty Melvin). Figure 33.

Plants with a single large tuberous root. Stems cryptic and grayish, and seem to mimic dead branches of shrubs or trees; stems mostly few-branched, to 1.5 m tall, and about 2 cm diameter. Seedlings and youngest plants with 4 ribs, older and adult plants with 4 or 5 (rarely 6) ribs or angles, the stem surfaces purplish brown and minutely pubescent with short, whitish hairs. Flowers large (15–22 cm long) and white with a long tube; spectacularly fragrant, opening shortly after sunset and visited by pollinating hawk moths (Sphingidae), and quickly wilting after sunrise. Fruits ovoid, 10 × 4 cm, bright red throughout, the pulp juicy and sweet. Flowering occurs synchronously in a population on one to few nights in July, the fruits generally ripening August and September, and rarely persist until spring (e.g., March).

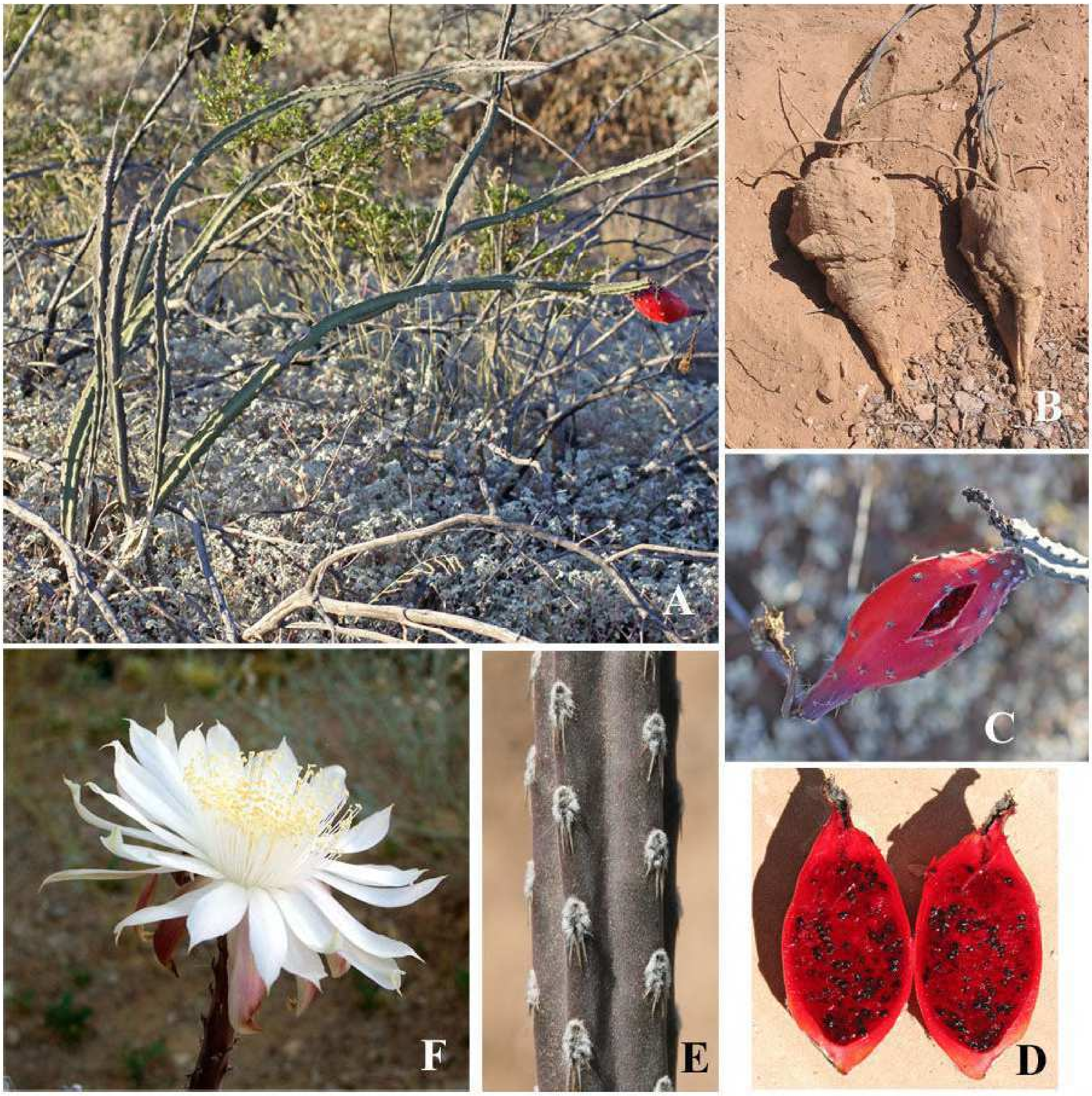

Figure 33. *Peniocereus greggii* var. *transmontanus*. (A & C) Kuakatch Wash west of Hwy 85, 6 Oct 2012. (B) Tuberous roots of plants rescued from construction site along Hwy 85, 9 Aug 2003. (D) Armenta Ranch Road, W of Hwy 85, 1 Mar 2008. (E) Dos Lomitas, 30 Sep 2006. (F) Organ Pipe visitor center, 14 Jun 2004.

Small to moderate-sized populations occur across Organ Pipe and Cabeza Prieta, mostly in the lowlands, separated by large unoccupied areas, and also in the Tinajas Altas Mountains. Creosotebush flats, bajadas, wash margins, canyons, and rocky slopes. Often growing in the shelter of desert shrubs, but sometimes also found in open areas (perhaps nurse plants were once present). The plants are seldom encountered due to the cryptic nature of the stems and throughout its range it characteristically grows at low densities. The stems are susceptible to freezing, but regrow rapidly from the large tuberous root. The plants are palatable to wildlife and packrats are known to chew the stems like a Popsicle. Illegal collecting has occurred in Organ Pipe along the US/Mexico border near populated areas.

Variety *transmontanus* is largely a plant of the Sonoran Desert in southern Arizona and northwestern Sonora. Variety *greggii* is a Chihuahuan Desert taxon, in southeastern Arizona, southern New Mexico, west Texas, Chihuahua, northeastern Durango, Coahuila, and Zacatecas.

The root has been used medicinally for diabetes and respiratory ailments, and the fruits eaten fresh (Felger et al. 1992). In his field notebook (Mearns 1892–93) recorded this: "The root is a large tuber, like a yam. In much repute as a remedy for syphilis throughout northwest portion of Mexico." Betty Melvin (in Zepeda 1985: 78–79) reported, "Well you get the root, and then you peel it. . . . and you wash your hair with it. . . . you peel them and you cut them up and they taste like. . . cucumbers. You eat it with meat. Ho'isa, that's the name." Castetter and Underhill (1935: 18) reported that the tuberous root was "chewed raw for thirst or . . . baked whole in ashes, peeled and eaten." Castetter and Underhill also claimed that the "stalks" were eaten, but that seems improbable.

OP: Bates Well, *Nichol 27 Apr 1939* (ORPI). 9 mi W of Visitor Center, N end of Puerto Blanco Drive, desert flats, 25 Nov 1972, *Pinkava 10034* (DES). Vicinity of Aguajita Spring, 3 Dec 1990, *Felger 90-574*. W of Hwy 85 on Armenta Rd, *Anderson 15 Jul 2002* (ORPI). Observations: Dos Lomitas, 30 Apr 2002, *Rutman*; 5 mi E of Quitobaquito in *Atriplex polycarpa* flats, Jan 1990, *Robert A. Johnson*.

CP: Near Jose Juan Represo, 12 Jun 1992, *Felger* (observation). Near Tule Tank, 5 Mar 1995, *Rebman 2890* (ASU). Western Tule Mts, rooted in bedrock, 25 Nov 2003, *Rutman* (photo).

TA: Tinajas Altas: 21 Feb 1894, *Mearns 2811* (DS, US); 6 Mar 1937, *Harbison 16828* (SD). E end Tinajas Altas Pass, 12 Feb 1977, *Reeves 5396* (ASU).

Peniocereus striatus (Brandegee) Buxbaum
[*Cereus striatus* Brandegee. *Wilcoxia striata* (Brandegee) Britton & Rose. *Neoevansia striata* (Brandegee) Sánchez-Mejorada. *Cereus diguetii* F.A.C. Weber. *Wilcoxia diguetii* (F.A.C. Weber) Diguet & Guillaumin]
Dahlia-root cereus; *sacamatraca, sarramatraca*; 'i:kulĭ. Figure 34.

Plants often 0.6–1.5 m tall and much branched above. Stems 4.5–8 mm diameter (1–2 years old), at first greenish with minute hairs, soon becoming brownish or grayish and glabrous, with 6–9 flat ribs separated by deep furrows or grooves, the stomata restricted to the grooves. Each plant may produce a dozen or more potato-like tuberous roots strung on clusters of slender connecting roots. (Plants in southwestern Sonora sometimes have up to 70 or more tuberous roots.) Areoles circular, ca. 1 mm diameter; spines 5–15 per areole, 1–5 mm long innocuous and bristle-like, mostly soon deciduous, (spines on floral tube and fruits much longer), white or brown-tipped, and closely appressed to the stem. Flowers nocturnal, about 9–11 cm long, 8+ cm wide, with a slender tube, the inner tepals white or moderately rose-tinted; pollinated by hawk moths (Sphingidae). Fruits about 5 cm long, ovoid, the ripe pulp red, juicy, sweet and edible, the rind red when ripe, with short bristly spines on small, sparsely distributed and deciduous areoles. Seeds 2–2.5 mm long, dark red-brown to blackish. Flowering in summer, the fruits ripening late summer and fall. Most of the plants show recovery from freeze-damage and herbivory.

Figure 34. *Peniocereus striatus* and *Euphorbia cryptospinosa*. *P. striatus*: (A) Bush-like form, Dos Lomitas, 15 Nov 2002; (B) 24 Oct 2007, photo by Jergen Mentzel (SEINet); (C) ripe and near ripe fruit, Dos Lomitas, 15 Nov 2011; (D) tuberous roots, Dos Lomitas, NPS-ORPI photo, 1940s; (E) Dos Lomitas, 15 Nov 2002, photo by Greta Anderson; (F) cross-section of stem, cultivated plant, originally from vicinity of Sonoyta, Sonora, 14 Aug 2013, photo by Elroy Limmer. *E. cryptospinosa*: (G & H) Cross-section of stem and portion of stem near apex with flower clusters (cyathia), cultivated plant, originally from Kenya, 14 Aug 2013, photos by Elroy Limmer.

Highly localized in the southeastern part of Organ Pipe near the international boundary where it is at its northern geographic limit, and farther east along the southern margins of the Tohono O'odham lands. There are no other populations in the United States (Felger & Zimmerman 2000; Rutman & Anderson 2007). The main population is in northwestern Mexico where it is widespread and sometimes locally common in western Sonora, northwestern Sinaloa, Baja California Sur, southern Baja California, and a number of Gulf of California islands (Felger & Wilder 2012; Suzán et al. 1994). The tuberous roots have been used medicinally (Felger & Moser 1985; Hodgson 2001).

Greta Anderson conducted an extensive study of this cactus in Organ Pipe from January to July 2002 (Anderson et al. 2010). Her study, covering 177 ha, included the known distribution within the Monument, which has been censused occasionally since 1939. Anderson found two growth forms among the Organ Pipe plants: vine-like and bush-like. Vine-like plants often scramble through spiny shrubs such as *Lycium* and tree branches for support, and can reach several meters across. Bush-like plants are sometime in open areas (not among a nurse plant, or perhaps the nurse plants has since perished) and the stems of such plants tend to show more than usual freeze-damage. The study resulted in the discovery of 88 new plants, in addition to the relocation of 57 plants found in previous surveys (Johnson et al. 1990). Mean height and width of the plants was 58.6 cm and 54.4 cm, respectively, the majority being 40–80 cm tall, and maximum height and width 158 and 304 cm, respectively. Despite potential increases in population size and spatial distribution, mean plant height and number of basal stems had not significantly changed in recent years. *Peniocereus striatus* occurrence increased with decreasing slope, spanned every slope aspect, and was highest on rocky temperature at the site dropped to -13.7°C, top-killed 19% of the population, with the greatest damage in drainage bottoms. However, long-term (1944–2002) climate records show that there has been an overall increase in the number of frost free days in the region, which, coupled with land use change, has implications for the future health of this population." By early summer 2002, more than half of top-killed plants had re-sprouted from the base or had new branches growing from the desiccated stems.

Greta's study came to an abrupt end on August 9, 2002 when her vehicle at the *P. striatus* site was vandalized by fugitives from Mexico on the day National Park Service Ranger Kris Eggle was murdered by one of the same two armed fugitives who had fled across the border into Organ Pipe. From Tim Tibbitts (13 Mar 2013): "My memory is Greta's incident was a couple hours before Kris was killed. I was at work, driving up out of Growler Pass, and heard it over the radio. I talked to Greta on the radio, drove to HQ, looked at her truck which had the window smashed out, spoke with Bo Stone, one of our law enforcement staff at that time, about getting the incident report taken care of. Around 1:00 pm, I headed north toward Ajo on the highway, headed home. Unbeknown to me (because I'd turned my radio off, in Off-Duty Friday mode), at about that time the shooting incident was playing out near Gachado."

The 2010 publication is dedicated to National Park Service Ranger Kris Eggle (1973–2002).

OP: 8 mi NE of Sonoyta, Sonora, 1400 ft, *Nichol 20 Apr 1939*. E of Lukeville, 1450 ft, *Nichol 4 May 1939* (ORPI). Dos Lomitas, 1500 ft, W-facing rocky hillside, with *Cereus thurberi, C. giganteus, Larrea tridentata, Ambrosia deltoidea*, growing in and among *A. deltoidea*, 63.5 cm tall, 16 Aug 1988, *Baker 7621* (ASU).

Sonora: 6 km E Sonoyta, cerca de la frontera con Organ Pipe Cactus National Monument, laderas riolíticas, 31°52'N, 112°45'W, 438 m, *Larrea tridentata, Encelia farinosa, Olneya tesota, Cercidium microphyllum*, 21 Oct 1993, *Suzán 333* (ASU).

CONVERGENT EVOLUTION OF *PENIOCEREUS STRIATUS* AND AN AFRICAN *EUPHORBIA*

The unusual stem morphology of *Peniocereus striatus* shows remarkable convergent evolution with *Euphorbia cryptospinosa* Bally (Euphorbiaceae), a spurge known from arid regions in Ethiopia, Somalia, and Kenya (Felger & Henrickson 1971; figures 34–37). These similar appearing succulents share water-conserving adaptations. The cactus and the euphorbia both have slender pencil-like stems with stomata restricted to furrows separated by bark-covered ribs. As the stems shrink in drought, the ribs come together to close off the furrows resulting in a cylinder-like surface, which effectively reduces water loss and surface-to-volume ratios (figures 35 & 37). Theoretical surface-to-volume relationships in succulent plants, especially cacti, are expertly described and interpreted by Mauseth (2000) and Porembski et al. (1991).

The cactus has stems 5–9 mm diameter and 6–9 furrows. The spurge has stems 7–12 mm diameter and 4–9 furrows. Both have brownish gray stems that look like woody stems or dead twigs of the surrounding shrubs, which presumably provide protection from herbivores through camouflage. Both have tuberous roots that provide water and food-storing capacity. The cactus has areoles that bear weak spines and relatively large, dioecious, nocturnal flowers (figure 36 a–d). The spurge bears only two spines (modified stipules), about 1.5 mm long at each node, is monoecious, and bears clusters of scarlet-colored cyathia near the stem-apex (Figures 34 G & H; 36 e–i).

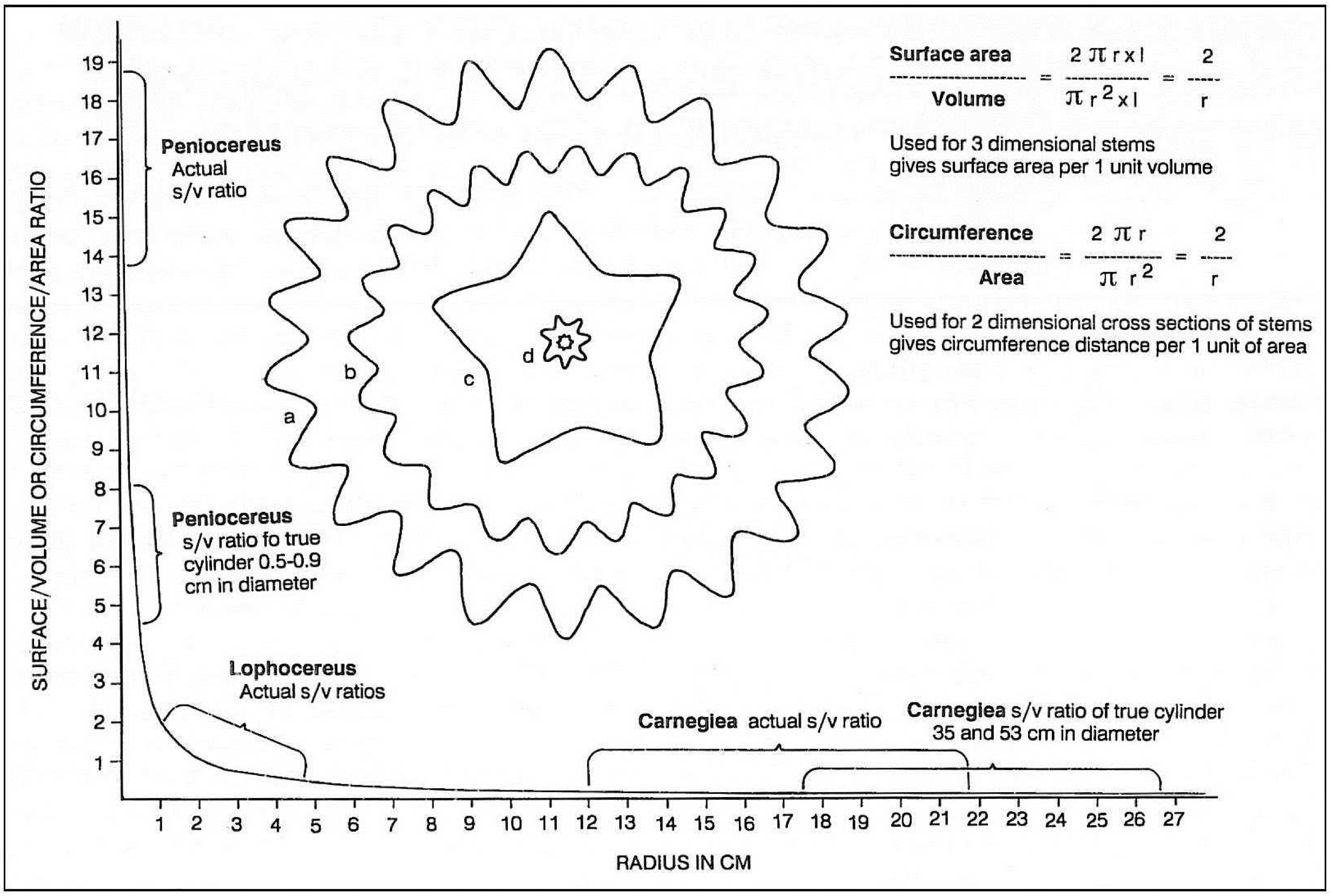

Figure 35. Relationship of surface/volume ratios and stem sizes. Formulas for determining three-dimensional surface/volume ratios and two-dimensional circumference/area ratios are shown at upper right. The curve on the left and bottom margin shows the relation between s/v ratio (ordinate) and stem size (as radius in cm, abscissa). (a–d) Outlines of various cacti from which s/v ratios have been determined: (a & b) *Carnegiea gigantea*: (a) larger stem; (b) smaller stem. (c & d) *Lophocereus schottii* showing extreme variation in stem sections from northern (c) to southern (d) populations (from Felger and Lowe 1967). An outline of a *Peniocereus striatus* stem is shown within d. The range of s/v ratios for the three cacti is shown along the regression curve. (From Felger & Henrickson 1997).

Numerous structural similarities exist at the microscopic level. In both, the ribs are covered with thickened, suberized, translucent periderm. The outermost cortex contains layers of collenchyma that are much thicker under the ribs than under the furrows. Collenchyma tissue in both species contains reddish pigment that darkens the outer stems, aiding in camouflage. The inner mass of cortex consists of parenchymatous water-storage tissue, while starch is stored in the pith.

In both species phellem (true bark) of successive seasons is eventually lost, falling away by means of an abscission layer comprised of thin-walled, non-collapsed cells that are the last-formed cells of the previous season's growth. Also in both species the consistent radial orientation of the phellem cells of successive seasons indicates that either the same phellogen is active over several seasons or new phellogens are derived from the phelloderm. The underlying lamellar collenchyma tissue present in both taxa consists of one or two layers (to 50 μ thick) of cells of dimensions similar to those of their respective phellem cells. Interior to the collenchyma tissue, parenchymatous cortex tissue contains chloroplasts that are more numerous under the ribs than under the adjacent furrows. Structure of the furrow region is distinct from that of the ribs, as the epidermis is persistent and is not replaced by more rigid periderm.

Yet the two species differ in many anatomical details. The rib periderm of *Peniocereus striatus* ranges from 35–50 μ in thickness and consists of tabloid cells 35–140 μ long and 30–40 μ wide, with moderately thickened walls. Rib periderm in *E. cryptospinosa* is slightly thicker (50–75 μ) and consists of longer, fiber-like cells to 450 μ in length, 25–50 μ maximum width, with uniformly thin walls.

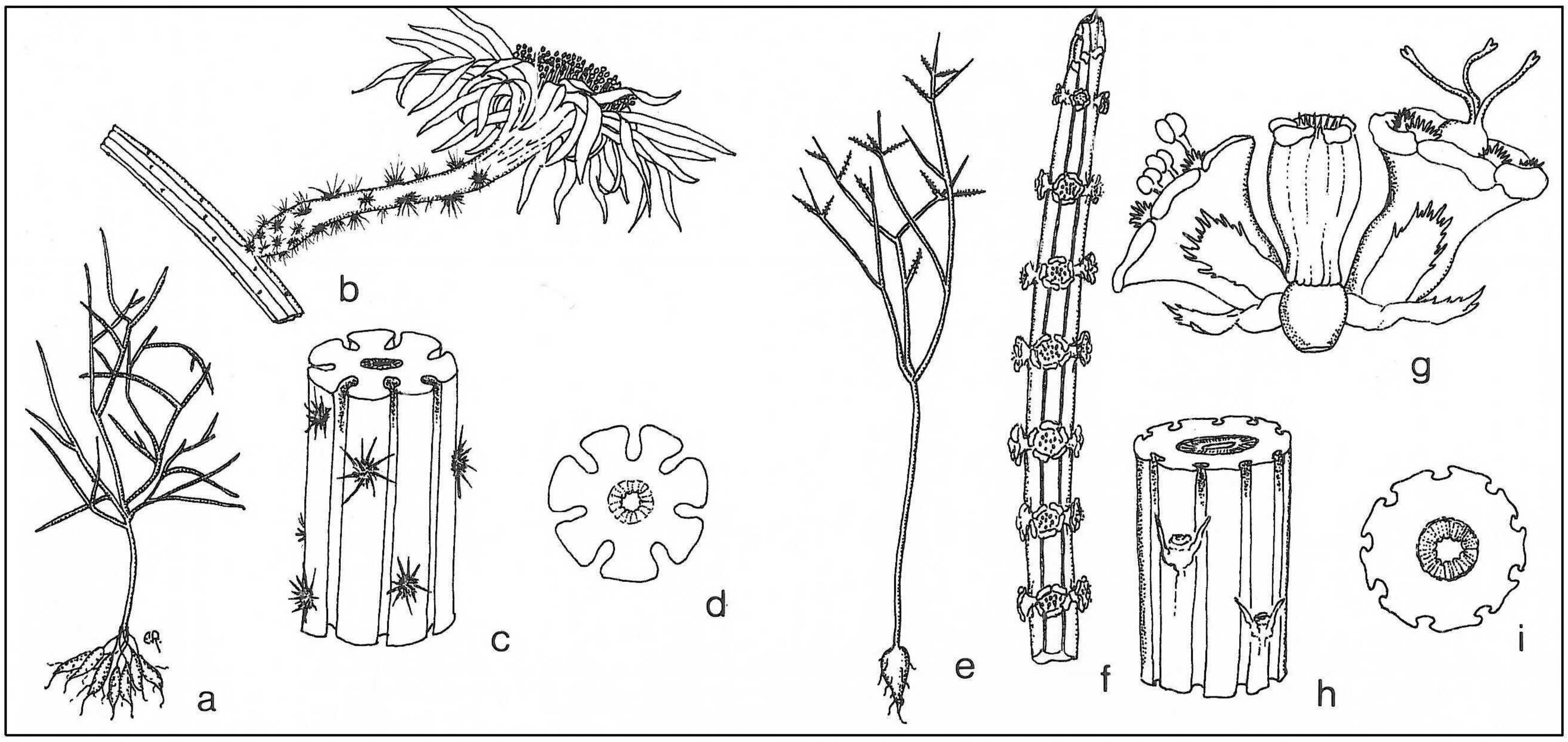

Figure 36. *Peniocereus striatus* and *Euphorbia cryptospinosa*. *P. striatus*: (a) growth habit; (b) stem with flower; (c & d) stem and cross section showing central xylem and stomata-containing furrows. *E. cryptospinosa* (redrawn from Bally 1963): (e) growth habit showing a single turnip-like storage root and branched stems; (f) distal portion of stem showing cyathia; (g) triad of cyathia, cyathium at left shows staminate florets (anthers) and cyathium at right shows a pistillate floret; (h) portion of stem showing paired stipular spines at nodes and distinctive furrows; (i) cross section of stem, showing central xylem and stomata-containing furrows. (From Felger & Henrickson 1997).

Minor structural differences are also apparent in the furrows. In *Peniocereus striatus* the outer epidermal cell walls are much thicker (14 μ) than the inner (3 μ) walls, with a thin cuticle measuring only 2 μ in thickness. Epidermal cell walls of *E. cryptospinosa* are also thickened but are considerably thinner (2–6 μ), while the cuticle is thicker (4 μ). The furrows of *P. striatus* are glabrous, while those of *E. cryptospinosa* are beset with short, blunt, biseriate trichomes to 80 μ long.

Stomata in both species are restricted to the furrow areas, with paracytic subsidiary cells. However, the cactus averages 48 stomata per mm^2, while there are 88 stomata per mm^2 in the spurge. Stomata along the furrow margins in desiccated stems of *Peniocereus striatus* are completely sealed over by an undetermined substance (perhaps a polysaccharide) that was removed by washing with water. This substance should be significant in reducing water loss during drought.

It's obvious that the internal volume of all succulents changes during wet and dry times or seasons. Expansion and contraction of stem volume typically alters the shape of the plant, e.g., ribs narrow, tubercles flatten or narrow, or, in most prickly-pears the entire stem flattens. The surface area remains approximately constant while the internal volume decreases, resulting in gradually increasing s/v ratios. But the stems of *Peniocereus striatus* and *E. cryptospinosa* provide a notable exception. During drought, volume (measured as stem cross-sectional area) decreases as expected. However, unlike other succulents, the effective surface area (circumference of the exposed area) also decreases as a result of the reduction of effective exposed surface area as the ribs close off the furrows. If the furrows are not closed off, the surface area in desiccated stems remains nearly unchanged and the s/v ratios would be 34–44 percent greater than those encountered. Moreover, because the exposed surfaces in the desiccated state primarily consist of impermeable periderm, the actual water loss is even less than might be expected from the s/v ratio alone.

It's remarkable that these two species have similar gross morphology, while each is distinct at the microscopic level. In desiccated stems of *Peniocereus striatus*, stomata at the margins of the furrows are sealed over by an unknown, water-soluble material. A similar phenomenon is seen in *Calabanus hookeri* (Nolinoideae, Asparagaceae), where similar water-soluble material fills stomata-containing furrows in the leaves of water-deprived plants. In contrast, furrows of *E. cryptospinosa* contain series of short, blunt trichomes or papillae that are similar in size and appearance to those found in such diverse semi-succulents as Joshua tree (*Yucca brevifolia*) and mistletoes (*Phoradendron brachystachyum* [*P. diguetianum*] and *P. flavescens*). These papillae are expected to provide reduced air movement within the furrows, thereby reducing transpiration by preventing mixing of dry air with the more humid air within the furrows.

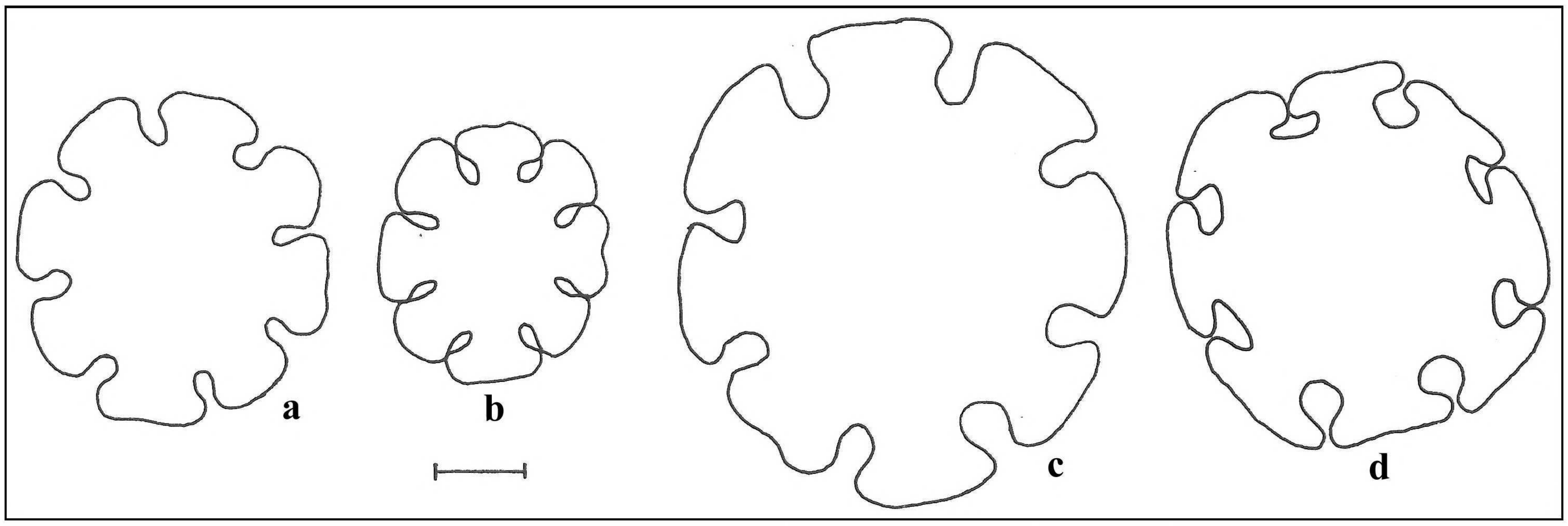

Figure 37. Outlines of hydrated vs. desiccated stems of *Peniocereus striatus* and *Euphorbia cryptospinosa*. *P. striatus*: (a) hydrated stem showing open furrows; (b) desiccated stem showing closed furrows. *E. cryptospinosa*: (c) hydrated stem showing open furrows; (d) desiccated stem showing closed furrows; bar = 2 mm. (From Felger & Henrickson 1997).

The stem structure displayed by *Peniocereus striatus* and *E. cryptospinosa* also occurs in other plants. Other related cacti also have narrow, furrowed stems, namely *Peniocereus lazaro-cardenasii* (J.L Contreras et al.) D.R. Hunt, *P. viperinus* (Weber) Buxbaum, and *P. zapilotensis* (Meyran) Buxbaum. Similar furrows and ridges are found in species of, trailing to climbing cacti ranging from Texas to northern South America. Stems of *S. murrillii* Britton & Rose have 7–8 periderm-covered ribs and the stomata are restricted to the furrows as in *P. striatus*. A number of East African spurges have similar stem morphology to that of *E. cryptospinosa* and *P. striatus*, e.g., *Euphorbia asthenacantha* S. Carter (Tanzania), *E. erlangeri* Pax (northeastern Kenya), *E. migiurtinorum* Chiovenda (eastern Ethiopia), *E. ataruensis* S. Carter (southeastern Kenya) and probably more (Bally 1963; Peter Bally pers. comm. to Felger, 1996; Robert Webb, pers. comm. to Felger, 2014; also see Carter 2001). *Euphorbia cryptospinosa* becomes a large shrub in the wild and the others are much smaller and likely to more closely resemble *P. striatus*. Also see comparative information for saguaro (*Carnegiea*) and senita (*Lophocereus*) (figure 35).

Sclerocactus – Pineapple Cactus

Small, usually globose or cylindrical plants. About two dozen species in southwestern United States and Mexico. Comparative DNA sequencing by Mark Porter at Ranch Santa Botanical Garden indicates that species of *Echinomastus* should be placed within *Sclerocactus* (Porter et al. 2000; also Porter & Anderson 2011).

Sclerocactus johnsonii (Parry ex Engelmann) N.P. Taylor
[*Echinocactus johnsonii* Parry ex Engelmann. *Echinomastus johnsonii* (Engelmann) E.M. Baxter. *E. acunensis* W.T. Marshall, Saguaroland Bull. 7: 33, 1953. *E. erectocentrus* (J.M. Coulter) Britton & Rose var. *acunensis* (W.T. Marshall) Bravo. *Neolloydia erectocentra* (J.M. Coulter) L.D. Benson var. *acunensis* (W.T. Marshall) L.D. Benson. *See* Baker (2012b) for detailed listing of synonyms and publications.]
Johnson's dwarf barrel cactus, Johnson's bee-hive cactus. Figure 38.

Dwarf barrel cactus, usually with a solitary, nearly ovoid to ovoid-cylindroid stem, 6.5–13 (27) × 6.5–8.5 cm, with 21 prominently undulate ribs. Spines obscuring the stem surface; central spines (1) 2–3 (4) per areole, ascending and slightly curved, 2.5–4.4 cm long; radial spines 13–15 per areole, straight, spreading close to the stem. Areoles bearing 1 (2) pale yellow-brown glands, these to 1.5 mm diameter, and attended by ants. Flowers showy, 3.5–6 × 4–9 cm. Inner tepals 13–21 in number, (2) 3–4 × 0.75–1.5 cm, bright rose-pink with pale margins (varying somewhat in hue from plant to plant), basally blotched with maroon or chestnut extending 30–45% of the length of the tepal. Filaments yellow-green (chartreuse), contrasting with the rest of the flower; anthers pale yellow. Stigma lobes 10–13, pink to dull red, covered with unicellular papillae of bright green, brownish green, or pale golden green. Fruits 1.5–2 cm long, ellipsoid-cylindroid, greenish and slightly glaucous, moderately fleshy, dehiscent through vertical splits (often indehiscent on drought-stressed plants), and quickly drying; receptacle bracts scale-like, the margins erose. Seeds dark red-brown (nearly black), 2–2.3 × 1.6–1.9 mm, the surfaces regularly and minutely papillate; seeds with or without a very low dorsal crest. Flowering mid-March and early April; fruits ripening in April. The plants are self-incompatible and effective pollinators are several species of native bees.

This cactus is rare in Organ Pipe, where it is usually found on bedrock or thin soils, or occasionally on well-drained alluvium or colluvium, (Johnson 1992; Johnson et al. 1993). Most of the plants are found on open, exposed situations. In nearby Sonora the young plants are often found beneath small shrubs as well as at the base of larger *Sclerocactus* plants, which serve as nurse plants, and the plants are generally more robust in partial shade of nurse plants than in open sites (Felger & Zimmerman 2000). Sue Rutman found that seeds can be viable for several years. The numbers of this cactus have precipitously declined in Organ Pipe, most likely due to drought and stem damage

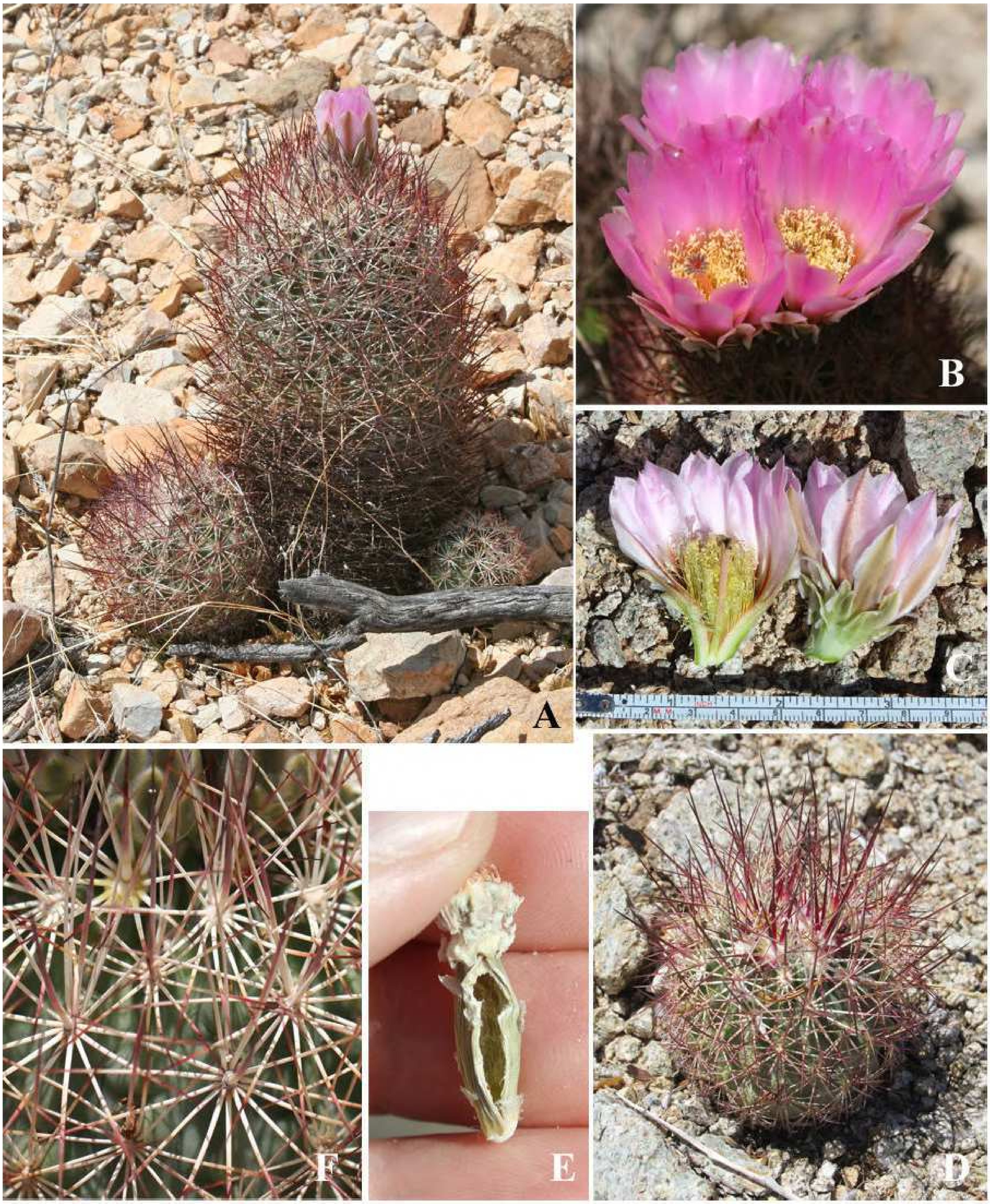

Figure 38. *Sclerocactus johnsonii*. Ajo, Pima Co: (A) Young plants established from seeds, at base of mother plant, east of Ajo mine pit, 19 Mar 2006; (B) 27 Mar 2010; (C) 11 Mar 2014; (D) spherical form of juvenile plant; (E) dry fruit, 23 May 2010; (F) 27 Mar 2010.

by boring insect larvae. Other sources of mortality are predation of seeds and fruits (by insects and birds), and loss by herbivory (perhaps by packrats, etc.), curved-bill thrashers uprooting plants, and poaching by cactus collectors (Organ Pipe Cactus National Monument 2011).

Arizona (widespread but spotty), northwestern Sonora, southern California (Mohave Desert), southern Nevada, and southwestern Utah.

Recent morphological evidence does not support the recognition of *Echinomastus erectocentrus* var. *acunensis* as a taxon unique from what we recognize here as *Sclerocactus johnsonii* (Baker 2007, 2012b). Marc Baker carried out an initial morphological analysis of *Echinomastus* in 2006 throughout most of its range in Arizona, California, and Nevada, sampling 476 individuals among 15 populations (Baker 2007). At the time of his study, populations of *E. acunensis* (basionym for *Neolloydia erectocentra* var. *acunensis*) were defined by Benson (1982) as occurring in Maricopa County south of Gila Bend; Pima County, Ajo and Organ Pipe areas; Pinal County, just east of Florence; and in northwestern Sonora. In Baker's study, discriminant function and cluster analyses placed populations of *E. acunensis* closer to those of *E. johnsonii* than to those of *E. erectocentrus*. For example, within the two southernmost populations of *E. johnsonii,* more than half of the individuals were misclassified as *E. acunensis* and there was only one individual of *E. acunensis* misclassified as *E. erectocentrus*. Since his earlier studies, Baker sampled two more populations of *E. johnsonii* (including the type localities for *E. arizonicus*, Butler Valley, Arizona, and *E. johnsonii*, near St. George, Utah) and results further supported the presence of a geographical/morphological cline from the northern Mojave Desert to the northern Sonoran Desert. Average character values, by population, for most characters decrease in value from the northwest to the southeast within the overall distribution of the populations studied. Results from this augmented analysis further support the inclusion of historical *E. acunensis* populations within *E. johnsonii* and suggest that there are no recognizable subspecific taxa within *E. johnsonii.* Although there was a fairly clear geographic and morphologic break between populations of *E. acunensis* and those of *E. erectocentrus*, there was no clear break between populations of *E. acunensis* and those of *E. johnsonii* (Baker 2012b). Based on Baker's findings, we believe that the status and final rule to list *Echinomastus erectocentrus* var. *acunensis* (U.S. Fish & Wildlife Service 2013) should be reviewed.

OP: Acuña Valley, rocky hills in open sun, cover type: creosote, *Supernaugh 2 Jan 1951* (lectotype of *E. acunensis*, DES; isolectotype, ORPI). Growler Mts foothills, S of Dripping Springs, 300 ft, 16 Apr 1952, *Parker 7983*. Acuña Valley, *Johnson 2 April 1989* (ASU).

Stenocereus

This genus includes 24 species of columnar cacti; southern Arizona to Honduras, West Indies, and northern South America.

Stenocereus thurberi (Engelmann) Buxbaum
[*Cereus thurberi* Engelmann. *Lemaireocereus thurberi* (Engelmann) Britton & Rose]
Organ pipe; *pitaya*, *pitaya dulce*; cucuvis. (Figure 39).

This stately cactus is the emblem for Organ Pipe Cactus National Monument. Multiple-stemmed, columnar cactus often 2.5–4+ m tall, the branches mostly arising from the base or near the base of the plant, and also often with some branching from the upper stems largely resulting from new growth from freeze-killed stem tips. Stems essentially homomorphic—lower and upper portions of stems similar (in contrast to *Carnegiea* and *Lophocereus*): stems 9–15.5 cm diameter at mid-stem height with ribs of low relief, (14) 15–17 (19) in number, or juvenile plants often with 12–14 ribs. Spines slender, spreading in all directions, longer spines 1–4 (5) cm, straight and needle-like (or occasionally a few spines are twisted); spines bright red as they emerge, quickly becoming dark and then ashy gray to nearly black—young areoles with dark red-brown glandular hairs, producing reddish-brown exudate that often coats the spines and becomes blackish within 1 or 2 years.

Flowers nocturnal, mostly May to July, sometimes flowering through August; flowers 7–9 × 6–7 cm, nocturnal, closing in the early morning; inner tepals white or pale pinkish lavender with white margins and bases; outer tepals and scales on the floral tube purplish red; nectar chamber relatively large and producing copious nectar. Stamens, style, and stigma creamy white. Fruits globose, 4–6.5 cm diameter, very succulent, indehiscent or splitting irregularly; pericarpel (skin and cortex) thin, red when ripe; floral remnant persistent. Occasional plants have golden-colored spines and produce yellow-spined fruits with yellowish pulp. Unripe fruits green and spiny, the spines lengthening before ripening; areoles readily fall away from the mature fruits, each fruiting areole with 18–32 spines emerging from a dense tuft of short, ribbon-like white hairs, the larger spines often 17–22 mm long, stout (0.4–0.65 mm diameter), usually slightly twisted, stiff, and grayish. Seeds 2–2.5 × 1.4–1.7 mm, blackish, with a weakly developed ridge along the "back." Fruit production (ripening) peaking in July and early August, and sometimes a minor fruiting peak again in September. Fruit pulp, seeds, and rind edible and delicious.

Widespread and common in Organ Pipe on rocky slopes, less common on gravelly bajadas and sandy flats, and on the east side of Cabeza Prieta mostly on granitic slopes and especially common in the Agua Dulce Mountains. In the Ajo Mountains it extends to about 4000 feet where it generally grows with *Juniperus arizonicus* and nestled among south- or west-facing rocks. The midden records probably reflect its arrival in the flora region about 3500 to 4000 years ago, at the beginning of the late Holocene, marking the formation of the modern Sonoran Desert plant communities.

Northern Sinaloa, southwestern Chihuahua, and most of Sonora to south-central Arizona, many Gulf of California islands, Baja California Sur, and southern Baja California.

The basal branching habit of the northern populations is apparently an adaptation to drought. Proceeding southward in Mexico the plants tend to branch higher off the ground, and south and southeast of the Sonoran Desert organ pipes are often arborescent with one or more trunks, and the plants are much larger than in the north. Conspicuous constrictions (scars), common on the stems among the northern populations, are the result of freeze damage and perhaps also drought (e.g., Parker 1987). The stem tip, where the surface-to-volume ratio is highest, is the part most vulnerable to freeze damage. The northern distribution is limited by freezing temperatures and the northwestern limits determined by aridity and more specifically by a paucity of summer rains.

In the thornscrub and tropical deciduous forest south and southeast of the Sonoran Desert in Sonora the organ pipes form well-developed trunks, branching occurs well above the ground, and the plants reach much greater heights than those farther north. Where vegetation is dense, as in the southern portion of the range in tropical deciduous forest, there may be an advantage in having the flowering stems above the forest canopy where they are accessible to bats for pollination and seed dispersal. Proceeding northward into the desert, the plants are progressively shorter until in the northernmost populations, such as in flora area, these cacti are trunkless and the branches arise at or near the base.

Pollination occurs during the night, probably primarily by the nectar-feeding lesser long-nosed bat (*Leptonycteris yerbabuenae*) and if open during daylight hours then primarily by the white-winged dove (e.g., Fleming et al. 1996). The long-nosed bat also feeds on the fruits and is a major seed disperser, and the cave floors of maternal roosts have thick deposits of organ pipe and saguaro seeds. The fruits are also consumed by birds (especially the white-winged dove), ants, and desert bighorn. Packrats (*Neotoma*) often create their middens around the bases of organ pipes, which provide protection and a ready source of food.

In Mexico the plant is known as *pitahaya* (*pitaya*). Some people, especially scholars, say that the plant should be called *pitahayo* (*pitayo*) and the fruit *pitahaya* (*pitaya*) (Santamaria 2000). In practice in Sonora, however, the feminine is in common use. In northwestern Mexico the woody

Figure 39. *Stenocereus thurberi*. Alamo Canyon, Ajo Mts: (A) Mouth of canyon, 9 Sep 2013; (C) 7 Apr 2005. Chuckwalla Hills: (B) 25 May 2006; (F) stem cross section of a fallen plant, 11 Feb 2009. (D) Young spines at stem tip, Organ Pipe plant nursery, 7 May 2006. (E) Estes Canyon, Ajo Mts, 25 May 2005. (G) Ripe fruit, W of Diablo Mts, Ajo Mt Drive, 2 Aug 2013.

stem ribs have served for house construction and fences, utensils, and many other utilitarian purposes. The Gachado Line Camp, a restored one room adobe building along the international border about 2 mi E of Lukeville (Broyles et al. 2007: 619), is the only known surviving example of organ pipe wood used in house construction north of Mexico. "A unique feature of the building is its ceiling and roof. Supported by cross beams and vigas, the roof consists of a layer of organ pipe cactus rib poles crossed by a layer of saguaro ribs. Over the saguaro ribs was placed a layer of cardboard, followed by one of creosote bush, then a layer of earth and blacktop" (National Park Service 2008).

Organ pipe fruits are highly esteemed by Sonoran Desert people and the fruit is commercially wild-harvested in southern Sonora and the fresh fruits sold in local markets (Yetman 2006). Unlike fruits of other columnar cacti in the Sonoran Desert region, the rind is relatively thin and edible, and the small seeds are edible along with the fruit pulp (Castetter & Bell 1937; Felger & Moser 1985; Felger et al. 1992). The fruit pulp was eaten fresh and also dried, or made into syrup and jam, and was especially relished for wine (Childs 1954; Felger & Moser 1985; Hodgson 2001; Betty Melvin in Zepeda 1985: 55). Just as they did for the saguaro fruit harvest, the Hia C'ed O'odham seasonally moved their residence for the harvest. Where numerous enough, organ pipe replaced saguaro fruit for ceremonial wine since it is sweeter, juicier, and tastes better. Lumholtz (1912: 331) reported that they "used to come as far as Quitovaquito and Santo Domingo to gather mezquite beans ... and eat sahuaro and pitahaya." Hia Ced O'odham "would collect the fruit of the organ pipe, and they would turn it into jam or else just dry it and eat it, eat it almost like candy" (Betty Melvin in Zepeda 1985: 55). The fruit continues to be a major wild harvested crop for Sonoran O'odham at Quitovac. The Presidential Proclamation establishing Organ Pipe Cactus National Monument in 1937 specifically allows the O'odham to continue their traditional harvest of fruits of the organ pipe cactus and other cacti.

OP: Cipriano Well, *Nichol 28 Apr 1939* (ORPI). 1 mi E of Bates Well, 1000 ft, 4 Mar 1940, *Benson 9900*. Quitobaquito, 14 Sep 1974, *Hodgson 14* (ASU). 2.4 mi W of AZ Hwy 85 on Puerto Blanco Drive, 2 mi NW of Lukeville, 19 Jun 1989, *Felger 89-221* (DES). 1.5 km S of Diablo Mountains, Ajo Mountain Drive, 13 May 1990, *Baker 7830* (ASU). 2.5 mi W of Hwy 85 on S Puerto Blanco Drive, 1500 ft, fruits with yellow spines, 11 Aug 1990, *Felger 90-402B*. †Puerto Blanco Mts, on ridge, seeds, modern (30) to 3480 ybp (11 samples).

CP: Ricks' Mine (Simmons 1965: photo, 2 June 1963). Agua Dulce Pass, 14 Sep 1992, *Felger* (observation).

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